AMERICAN MUSEUM NOVITATES

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CITY OF NEW YORK JANUARY 31, 1949 NUMBER 1400

THE HUMERUS FROM FISH TO MAN[1]

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CONTENTS

PREREQUISITE, PREADAPTIVE STAGES

The humerus, the bone of the upper arm, is not found in any animal phylum except the Chordata, and among the latter it is, of course, absent in limbless or snake-like forms.

The oldest known chordates, ranging from Ordovician to Upper Devonian times, belonged to the Class Ostracodermi, which even at that remote period were bilaterally symmetrical fishes (fig. 1) with segmentally arranged muscle flakes along the sides of the body. These myomeres were then the primitive locomotor organs, which have been transmitted with increasing modification to all later vertebrates. What is probably one of the oldest types of body form among the ostracoderms (fig. 1A) consisted of: (1) a rounded head shield, housing the brain and covering the mouth and branchial chamber, followed by (2) a muscular, thoracico-abdominal region, and (3) a muscular, tapering tail. The ventral surface was already more or less flattened, and the paired eyes

[1] Based partly on a paper read before the Viking Fund Conference on Locomotion, New York, February 7, 1948.

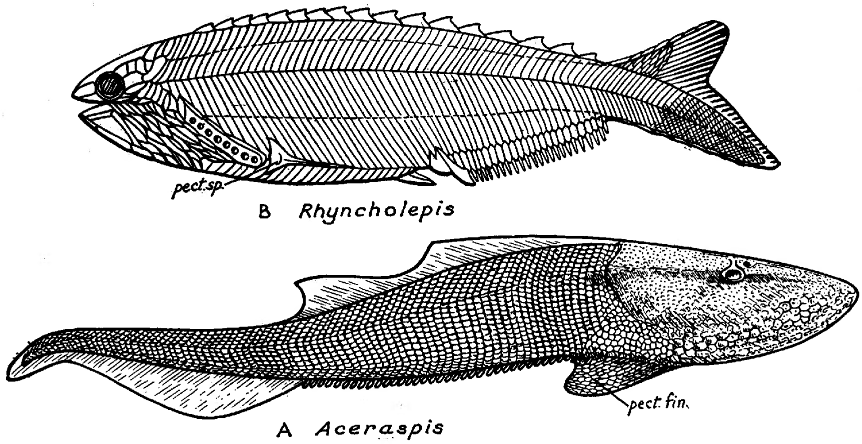


FIG. 1. Ostracoderms of Upper Silurian or Lower Devonian age. After Kiaer.

were either on the side of the mouth or on top of the shield. In some of the Pterapsida the body form, although somewhat flattened ventrally, was almost fish-like. In others it was dorso-ventrally flattened and more or less skate-like. In the Anaspida (fig. 1B), which were probably specialized for rapid swimming, the head shield was greatly reduced, exposing the large oralo-branchial region; the body was elongate, more or less laterally compressed. In all known ostracoderms the tail tip was turned more or less downward.

Both median and paired fins or lappets in the ostracoderms (fig. 1A), as in fishes generally, served mostly as cutwaters, bilge keels, and rudders, the main locomotor thrusts coming from the lateral muscles. In most of the cephalaspids there were more or less muscular extensions of the body wall at the outer rear margins of the shield (fig. 1A). These "pectoral fins" were supported by an "endoskeletal pectoral girdle" (Stensiö, 1927, 1932).

The exoskeleton in most ostracoderms, from the Ordovician *Astrapis* upward, was a highly organized complex of stratified, bony or near bony deposits, evidently a by-product of calcium metabolism. In Cephalaspida there was also extensive endoskeletal tissue as in the interbranchial septa and in the endoskeletal shoulder girdle (Stensiö, *op. cit.*). This endoskeletal tissue of the earlier chordates was doubtless the material out of which the humerus, along with all other bones of the paired appendages, was later fashioned.

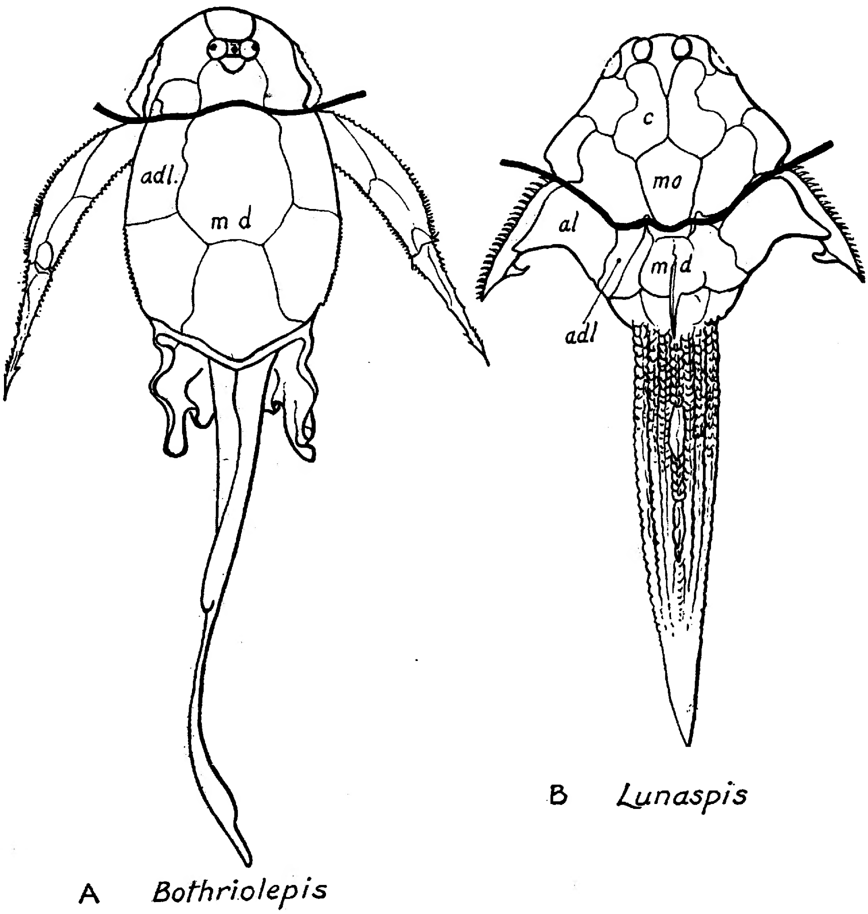


FIG. 2. Devonian antiarch (A) and macropetalichthyid (B). A after Patten; B after Broili and Schröder.

The Upper Silurian and Devonian Antiarchi, typified by the well-known *Pterichthys* of Great Britain and *Bothriolepis* (fig. 2A) of North America, had a rounded head shield, a large domed thorax, and a tapering caudal sweep. Their long, pointed, swimming appendages were covered with an elaborate system of dermbone armor plates and had neatly turned joints at the functional shoulder and elbow. The upper-arm piece articulated by a convex head, which was received into a goblet-like outgrowth from the anteroventral corner of the bony thorax. According to Stensiö (1931, pp. 111, 112) there was also an endoskeletal core with concentric layers of lime, at least in the upper arm, so that he re-

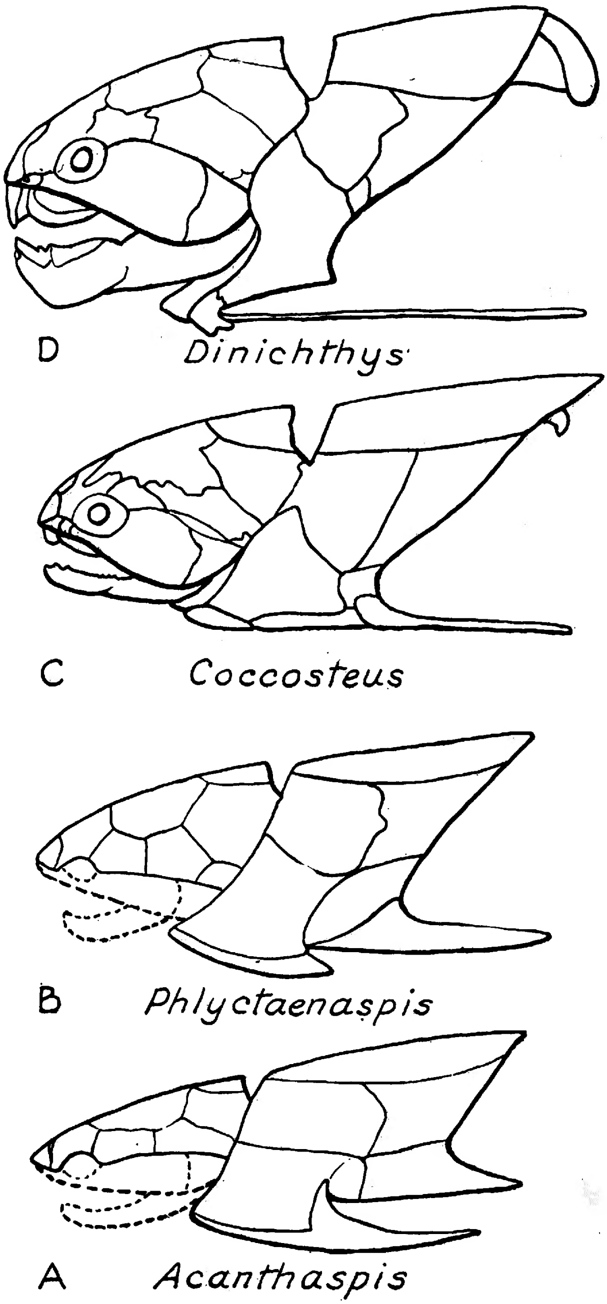


FIG. 3. Structural evolution of the head shield and thoracic buckler in acanthaspids and arthrodirans. After Heintz.

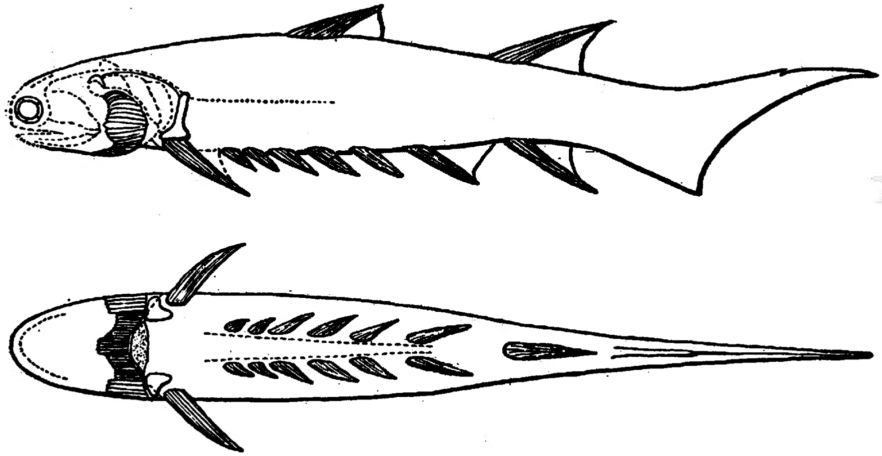


FIG. 4. Restoration of a primitive acanthodian. After Watson.

gards the entire organ as the homologue of the pectoral fin of fishes.

Among the Placodermata, also of Upper Silurian to Devonian age, we find a similarly wide range of body forms, including the shark-like Stegoselachia (fig. 2B), the skate-like Rhenanida, and the joint-necked Arthrodira (fig. 3). In general the less specialized forms (e.g., fig. 3B) had a well-developed bony head shield and thorax. In the arthrodires, as Heintz (1931) has shown, the bony thoracic shell shortened up (fig. 3C, D) until it looked like the exoskeletal shoulder girdle of bony fishes; while the pectoral appendages, already spike-like in the Acanthaspida (fig. 3A), dwindled into vestiges. In the Stegoselachia, on the contrary, both the pectoral and pelvic appendages were supported by endoskeletal pieces which collectively are remarkably like those of sharks (Broili, 1933).

The Devonian to Permian Acanthodii were formerly regarded as a peculiar side branch of the sharks, but Watson (1937) especially has shown that in some respects they are much more primitive than sharks in the structure of their skull, jaws, hyoid and gill arches. Their pectoral appendages (fig. 4) consisted chiefly of a pair of long spikes, apparently derived from minute, closely crowded and coalesced dermal denticles. At least in some acanthodians (fig. 5A) there was a web of skin near the base of the pectoral spine, and within this web were a few bony pieces which

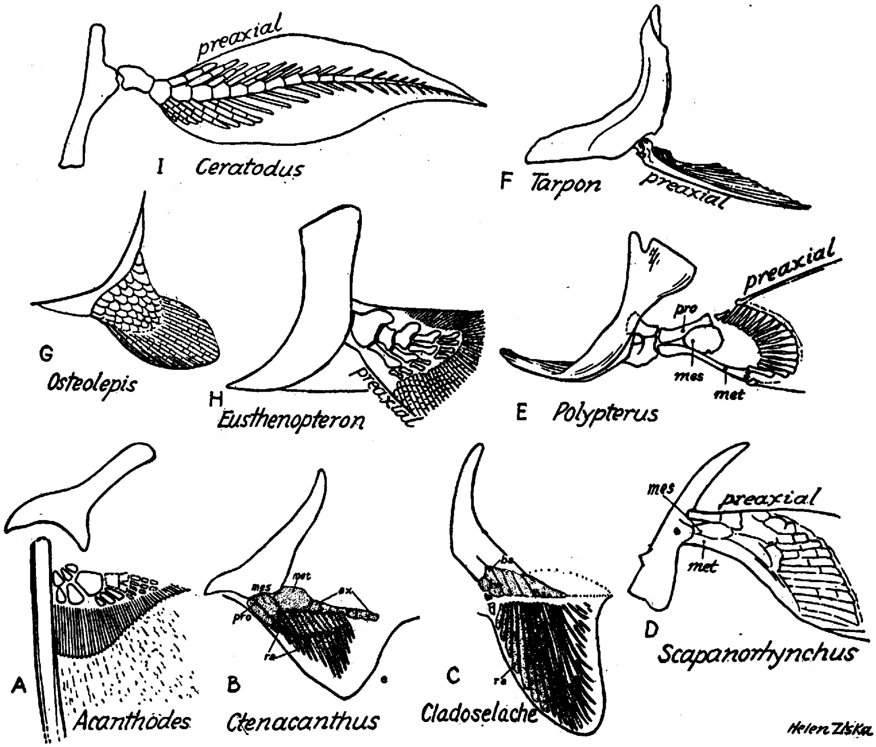


FIG. 5. Morphology of the pectoral fins. A. Acanthodian. B–D. Fossil and Recent sharks. E. Surviving ganoid. F. Modern teleost. G, H. Lobe fins (crossopterygians). I. Modern lung fish. From Gregory and Raven.

suggest the basals and radials of sharks. The pectoral girdle in acanthodians (fig. 4) may, as a whole, be homologous with the thoracic armor of placoderms (fig. 3). Ventrally it includes on each side several pieces which supported the pectoral spines, but the possible homologies of these pieces with the basal pieces of sharks and with the humerus of Crossopterygii (fig. 6B) are uncertain.

Heintz (1931; 1938, pp. 19–25) has suggested that among arthrodires the reduction and elimination of the large pectoral spines in coccosteid arthrodires might well have cleared the way for the expansion of the web and its supporting and activating rods, as in the macropetalichthyids. In the earlier acanthodians (fig. 4) as well as in certain anaspid ostracoderms the paired pectoral spikes form the first of a longitudinal series on either side.

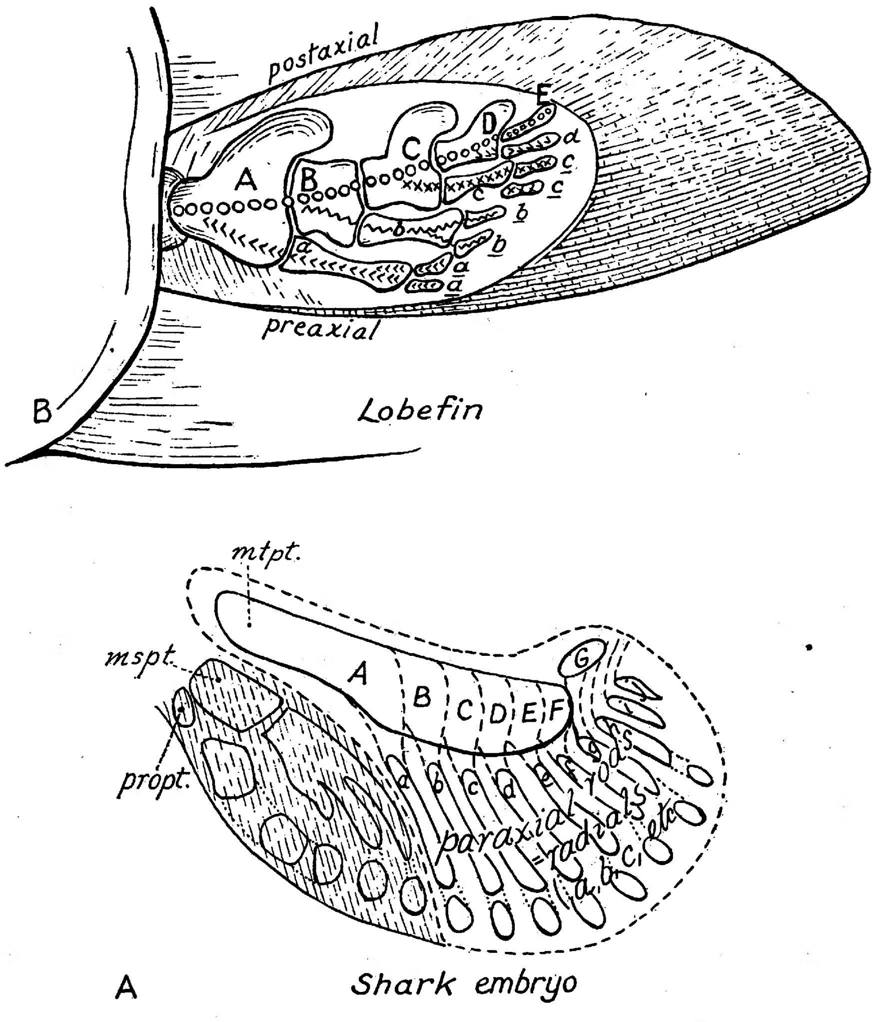


FIG. 6. Skeletal patterns of pectoral fins of lobe fin (B) and shark embryo (A). A after Moy Thomas; B after Gregory and Raven. In A the area with interrupted lines indicates the parts that are reduced or lost in B.

In the ventral view (fig. 4) these rows of spines converged towards the paired pelvic and median anal fins. Such rows of fins have been regarded as remnants of the spineless longitudinal finfolds of larval sharks and of the Upper Devonian shark *Cladoselache* (fig. 5C), but there is evidence for the very early emphasis of the exoskeleton in the great number of Paleozoic spine-bearing fishes, including macropetalichthyids, acanthaspids, acanthodians, and

true sharks, and there is further evidence for the reduction of spines in *Microbrachius* among the antiarchs and in the macropetalichthyids (*Lunaspis* to *Macropetalichthys*). Thus the spinelessness of *Jaymoytius* (E. I. White, 1946) and *Cladoselache* (Dean, 1909) may not safely be assumed as primitive. Moreover the absence of large paired fin spines in *Cladoselache* (fig. 5C) is associated with a general reduction of the exoskeleton (even the shagreen denticles being extremely small) and with a great multiplication of endoskeletal rods ("radials") which extend outward almost to the edge of the wide-based pectoral (fig. 5C) and pelvic fins. Doubtless these endoskeletal rods were secreted between the myocommata covering adjacent prolongations of the myomeres.

In typical sharks the radial rods converge medially towards three basal pieces, the propterygium, mesopterygium, and metapterygium (fig. 6A). Of these there is some evidence that the metapterygium is at least functionally analogous with a humerus.

THE FIRST TRUE HUMERI

A true humerus first appears in the Devonian Dipnoi and Crossopterygii. In the Dipnoi distal multiplication of the metapterygial units eventually produced a tapering, leaf-like paddle (fig. 7F), which in *Protopterus* (fig. 7G) and *Lepidosiren* became filiform. In *Neoceratodus* (fig. 7F) the diminishing cone-in-cone arrangement of the muscles that move the pectoral fin indicates their derivation by the successive budding of myomeres. An arrest of axial growth and a lateral spreading out of the series of pre-axial radials would approach the fan-like pectoral paddle of the rhipidistian Crossopterygii, as long ago noted by Braus (1901), Goodrich (1909), and others. In *Eusthenopteron* (fig. 6B) distal multiplication of the metapterygial segments had indeed ceased with the fifth mesomere (E), while the large proximal or humeral segment (A) grew wider and developed a strong distal-medial (entocondylar) process, probably for chevron-like muscles that fanned out towards the radials (a,b,c,d). Thus emerged (fig. 8A2, C) a single shoulder joint and a two-part elbow joint. The larger elbow joint (AB) was for the short, succeeding mesomere (B), analogous in position with an ulna (U); the smaller one (Aa) for a slender, rod-like, pre-axial piece (a) that suggests a radius (R).

These features were all prerequisites or preadaptations for the tetrapod humerus, but as in every other major transformation

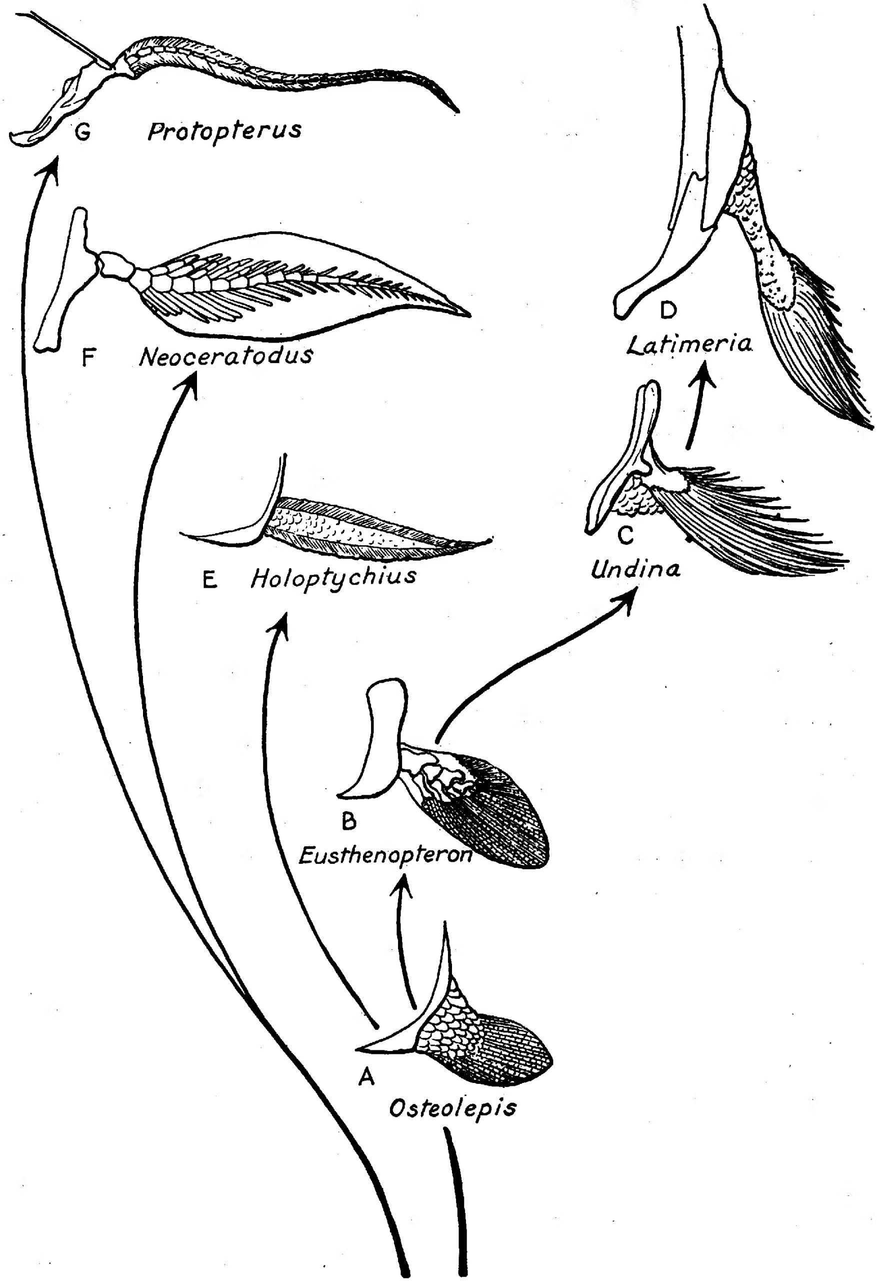


FIG. 7. Divergent evolution of lobe fins (crossopterygians) and dipnoans. After Gregory.

there were reductions and losses as well as new gains. That is, all the dermal rays had to be eliminated and possibly one or more of the pre-axial radial branches of the paddle were lost, while from the postaxial, digitiferous border (figs. 8–10) sprouted the second to fifth carpals, metacarpals, and digits (Gregory and Raven, 1941).

THE HUMERUS OF PRIMITIVE TETRAPODS

When the choanate ancestors of the amphibians crawled out and wriggled about on muddy flats, a strong bending of the pectoral paddles, especially between their first and second segments, corresponding to the elbow joint, would permit the more distal part of the paddle to be applied to the substratum (figs. 8–10). Thus the thrusts of the forelimb would help to steer the wriggling of the axial muscles and to raise the ventral surface a little from the ground. That a pectoral fin with a strong muscular lobe can be bent and twisted is seen in the African ganoid fish *Polypterus* which has stout and muscular pectoral paddles. The pectoral musculature, as figured by Klaatsch (1896) was essentially of the cone-in-cone type, that is, an extension of the segmental muscles of the body wall. Although it is uncertain whether or not the metapterygium of *Polypterus* (fig. 5E) is homologous with the humerus of *Eusthenopteron* (fig. 5H), the pectoral musculature of the former suggests a division into a proximal group corresponding to the zono-humeral muscles and a distal group running to the forearm and dermal rays. But this is a matter calling for further investigation.

In some of the early tetrapods, increasing multiplication of axial segments favored the wriggling movements of the body, and the paired limbs remained small or became reduced and disappeared, as in the serpent-like Aistopoda, the Caecilia, and many others. On the other hand, in the lines that led to the typical tetrapods, natural selection evidently favored a genetically determined increase in size, on the ventral side, of the pectoral and coracoid muscles and of the humerus itself. Dorsally a corresponding increase occurred in the scapulo-humeral muscles and in their insertion areas on the humerus.

The pectoral girdle and limbs of fishes are usually situated at or near the widest diameter of the body just behind the gill chamber (fig. 9A). The girdle itself is tied to the skull via the tabular, posttemporal, and supracleithrum. The very large cleithrum bounds

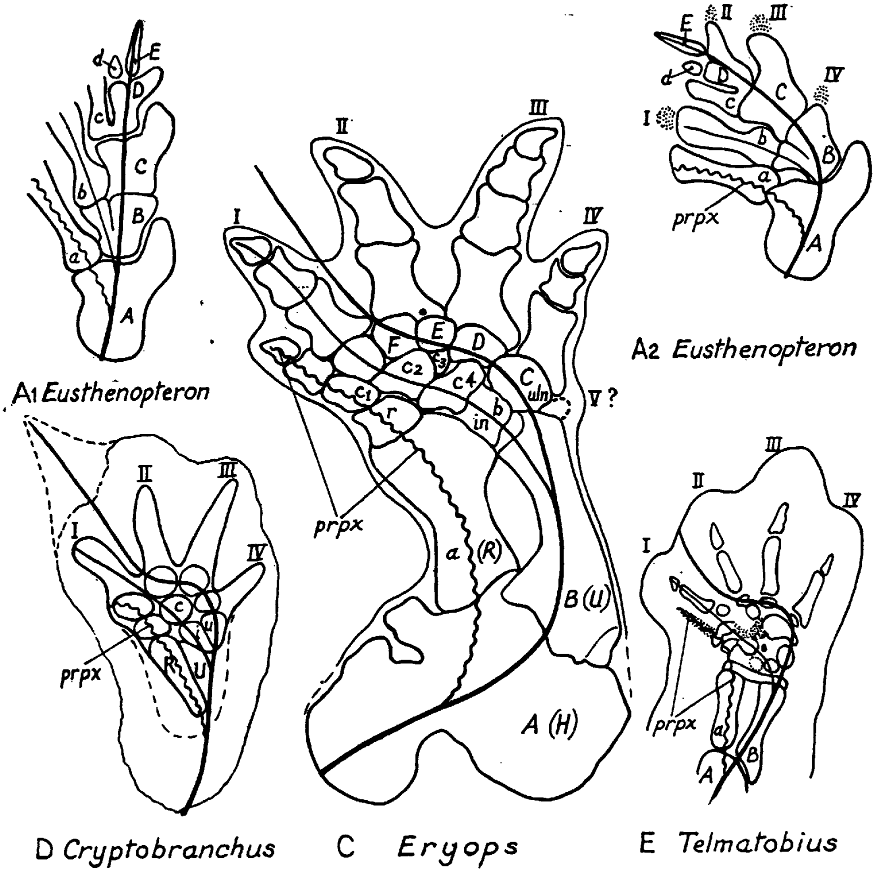


FIG. 8. Skeletal patterns of uplifted pectoral appendages. A1. Devonian lobe fin, indicating humerus (A) in relation to succeeding mesomeres (B–E) and pre-axial radials (a–d). A2. The same, but with sharp flexure at the elbow joint (aB). Dotted areas indicate inferred sites of budding metacarpals. C. Fully developed pectoral appendage of Carboniferous labyrinthodont. D. Pectoral appendage of embryo urodele. E. Pectoral appendage of larval anuran. After Gregory.

the gill chambers, affords an anchor for the lateral segmental muscles, and a base for the scapulacoracoid, mesocoracoid, and the pectoral limb. In the early tetrapod *Eogyrinus*, as Watson (1926) has shown, the pectoral girdle was still connected with the skull and the cleithrum was relatively very large. In typical tetrapods (fig. 9C), on the contrary, the connection with the skull is lost, the gill chamber is reduced and retreats to the ventral side, the cleithrum later dwindles to a vestige. The very large scapular blade,

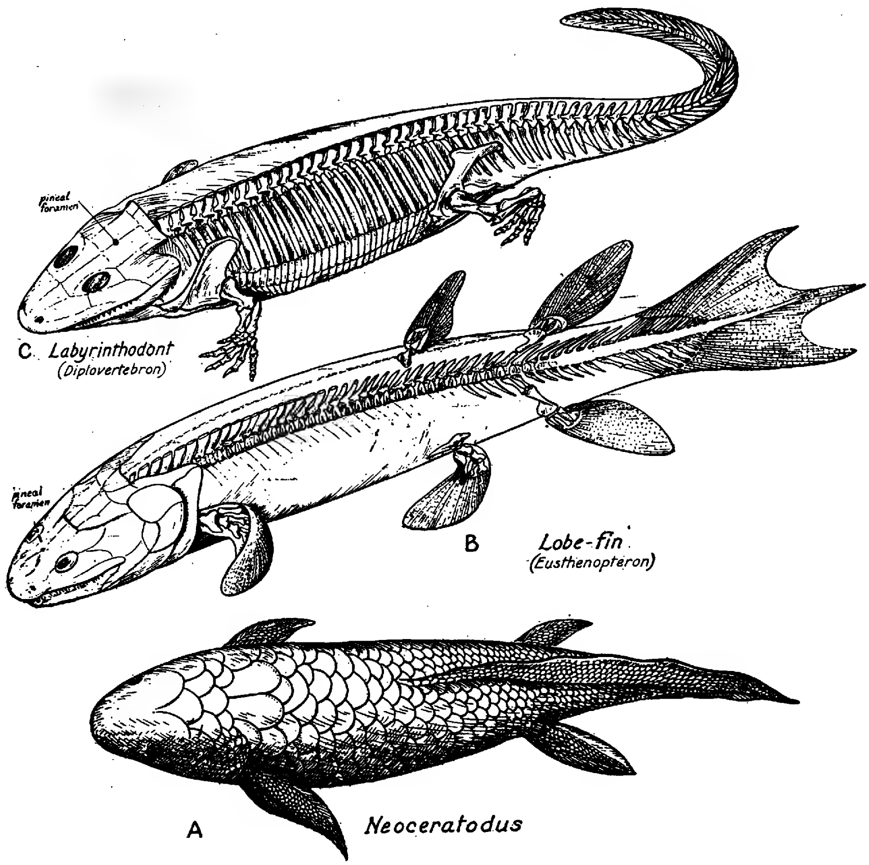


FIG. 9. A. Modern lung fish, oblique dorsal view, showing paired fins. After Gregory. B, C. Restorations of the skeletons of Devonian lobe fin (B) and Carboniferous labyrinthodont (C). B modified from Gregory and Raven; C from a model made under the author's direction, with data from Watson.

especially in heavy-bodied forms (fig. 13, A1), has grown far upward; meanwhile the coracoid has expanded and gained a firm base on the enlarged sternum. Thus the pectoral girdle, which arose in fishes as a transverse brace between the skull and the body and as an anchor for the muscles of the flanks, was later transformed into a U-shaped cradle for the support of the body on land, serving also as a base for the expanded and mostly fan-like muscles converging ventrally on the humerus.

Closely correlated changes occurred also in the humerus, as may be seen by comparing the relatively small and simple humeri

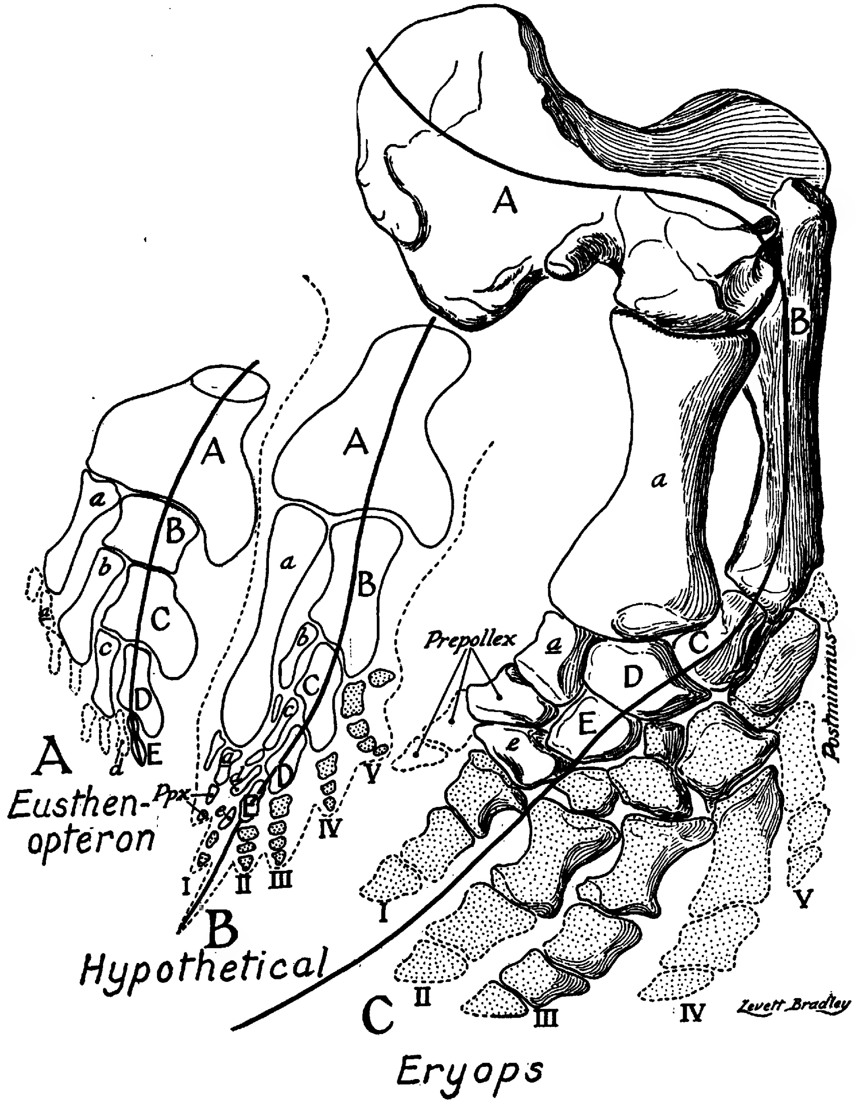


FIG. 10. Skeletal patterns of the pectoral limbs. A. Devonian lobe fin. B. Hypothetical intermediate. C. Permo-Carboniferous labyrinthodont. After Gregory and Raven.

of *Eusthenopteron* (fig. 10A) and *Sauripterus* (fig. 31) with the large and complexly built humeri of *Eryops, Diadectes, Dimetrodon,* and later forms.

Romer (1922, p. 554) showed that in primitive tetrapods the

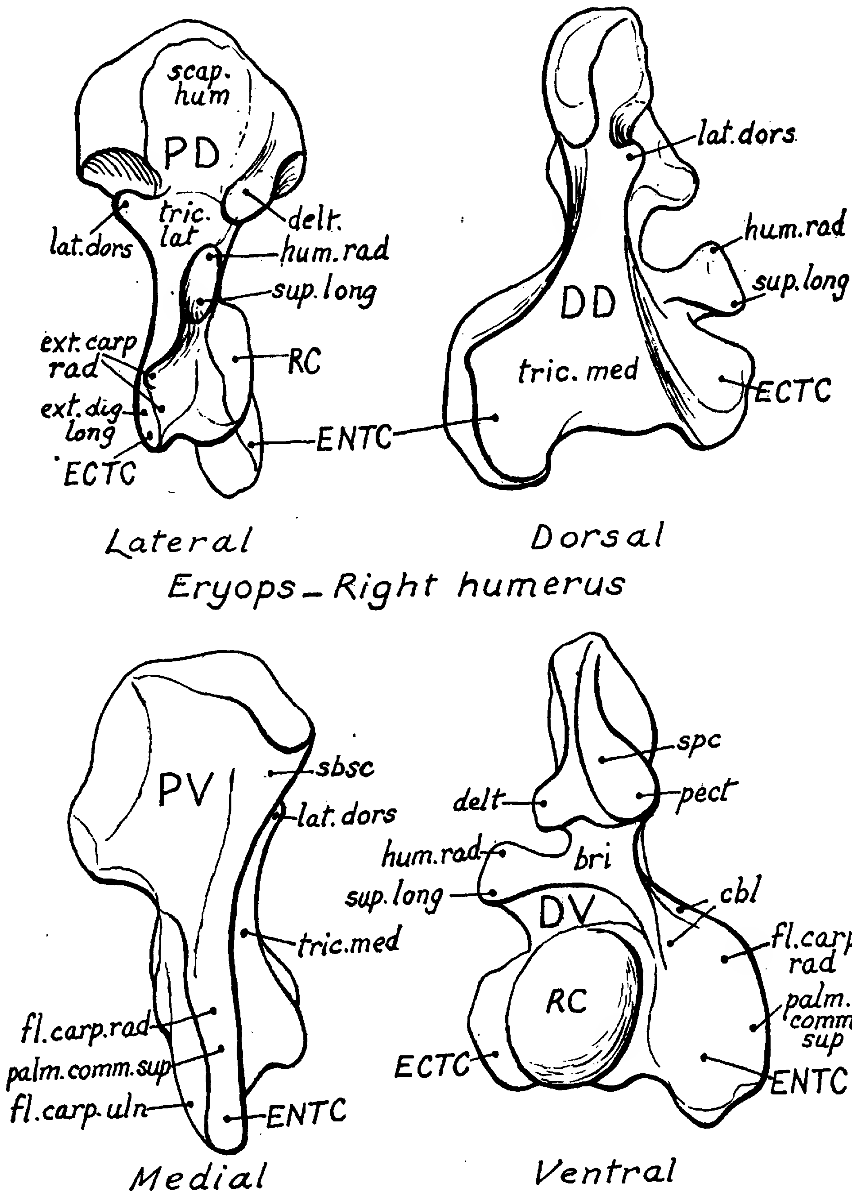


FIG. 11. Four views of the right humerus of a large Permo-Carboniferous labyrinthodont, to illustrate the four "triangular areas" of Romer. Humerus after Miner; triangular areas after Romer; muscle areas after Miner. PD, proximal dorsal; DD, distal dorsal; PV, proximal ventral; DV, distal ventral areas; ECTC, ectepicondylar process; ENTC, entepicondylar process; RC, capitellum for radius.

humerus, with its wide proximal and distal ends nearly at right angles to each other, "was built as a tetrahedron [fig. 11], composed of four roughly triangular surfaces, two having their bases proximally, and two distally, with the planes of these bases at right angles to one another." The tetrahedron is enclosed by four roughly triangular surfaces, respectively, proximal-dorsal (PD), distal-dorsal (DD), proximal-ventral (PV), and distal-ventral (DV). Each of these serves as a triangular truss, and collectively they resist bending moments imposed by muscular force, by weight, and by the reactions of the medium, converging towards the humerus from various directions. In very short humeri of primitive tetrapods (figs. 11, 14, 15) the wide bases and low height of the four humeral triangles reflect the relative thickness and shorter contractile ranges of their respective muscles or muscle groups, while the relatively long shafts of many later humeri (figs. 14, 15, 29) indicate reduced thickness and strength with lengthened contractile ranges. Emphasis of any of the cross sections, crests, or processes implies greater strength of muscles or ligaments and involves changes in their angles of insertion and in the lengths of their lever arms. For example, the very large entocondylar projection in primitive tetrapod humeri (fig. 11, ENTC), together with the shortness of the forearms (fig. 13A), implies (a) corresponding thickness and strength of the pronators and (b) relatively open insertion angles, with directions of pull more nearly at right angles to the shaft of the radius and thus with favorable leverage but short range.

The spirally warped head or proximal articular facet (fig. 11) of the primitive tetrapod humerus permitted partly rolling, partly twisting movement of the humerus under the pull of successive sectors of the fan-like muscles covering the neck and pectoral girdle (Miner, 1925). The capsular and other ligaments must obviously have been so arranged as to permit this rocking and twisting movement.

The primitive tetrapod humerus was adapted for a crawling gait, with sharply everted elbows, wide trackway, and short stride. It is best exemplified in large-bodied labyrinthodonts such as the Permo-Carboniferous *Eryops* (fig. 13A, A1) and in the diadectid division of the Cotylosauria or primitive reptiles. In humeri with lengthy shafts (figs. 14, 15, 29) the proximal and distal humeral triangles recede, and the humerus as a whole assumes somewhat the functions of a loaded beam supported at either end, or more

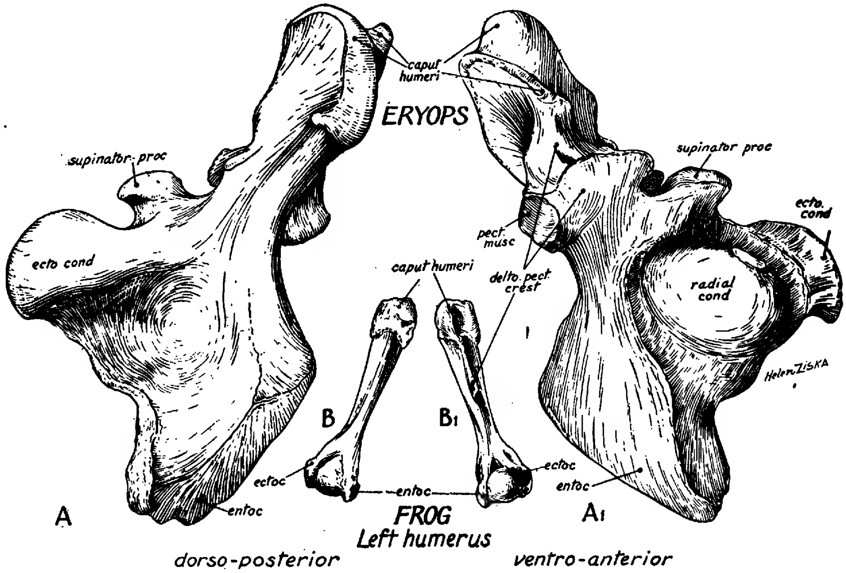


FIG. 12. Humeri of primitive tetrapod (A, A1) and modern anuran (B, B1). After Gregory.

specifically of the boom or jib of a derrick crane (fig. 30). When the head of the humerus (figs. 14, 15, 25) grows towards the dorsal or rear side the upper third of the bone may be bent backward, the lower third forward, producing a more or less sigmoid contour in side view. Strengthening of the bone may occur either by thickening the walls of the more or less hollow shaft or by the presence of old or new crests between the muscle masses. Successive cross sections from the surgical neck downward suggest a system of opposed (front and back) triangular struts or trusses (fig. 11).

SURVIVING AMPHIBIA

Among the smaller surviving Amphibia the ends of the humerus often became cartilaginous. In the urodeles (fig. 31) the usually small humerus is frequently associated with aquatic habits and with a wide, fan-like expansion of the coracoid cartilage and its muscles. The scapular blade sends forward a large "procoracoid" process which serves as a base for the fan-like supracoracoideus and procoraco-humeralis muscles. Reduction and loss of the cleithrum, clavicle, and interclavicle in these urodeles have contributed to considerable mobility of the right and left halves of the

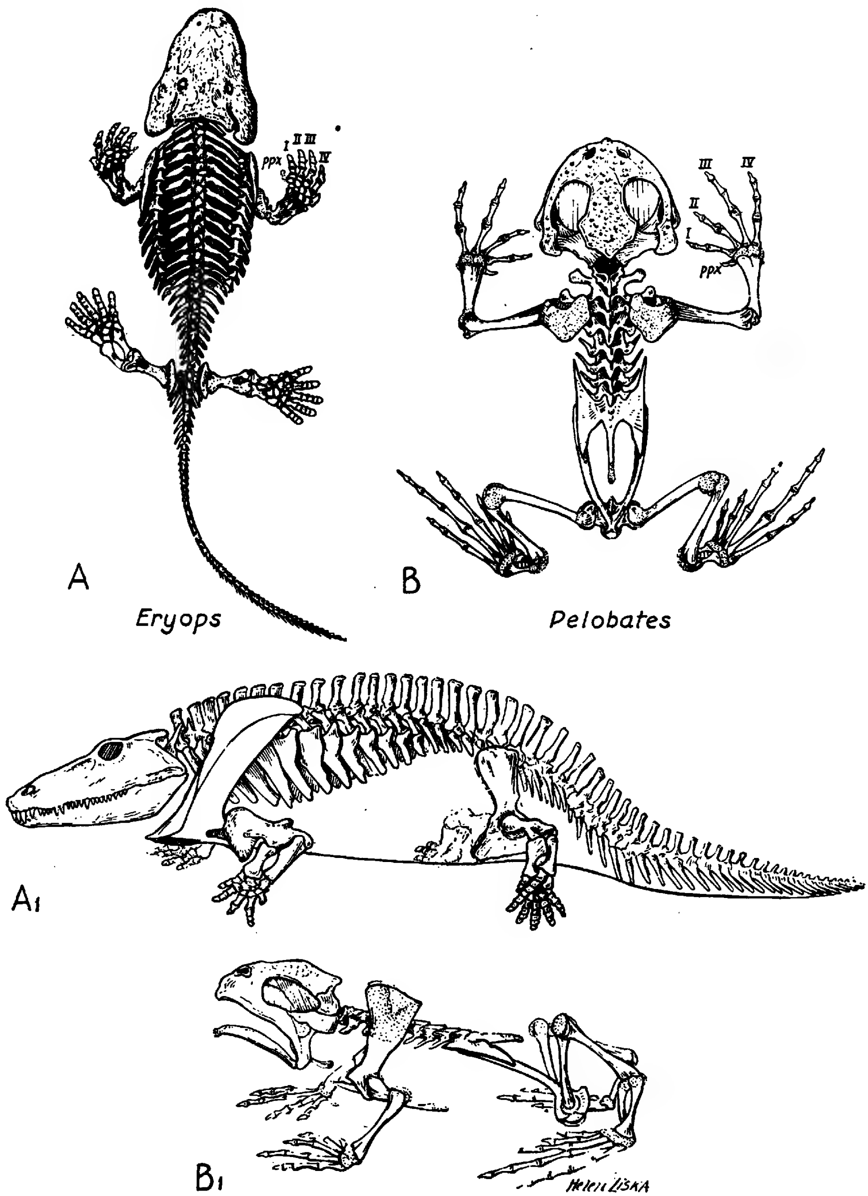


FIG. 13. Skeletons of primitive tetrapod (A, A1) and modern anuran (B, B1). After Gregory.

coracoscapular arch, to a widely swinging movement of the humerus and to a long reach in swimming.

In the frogs and allied forms (fig. 13B, B1) leaping and swim-

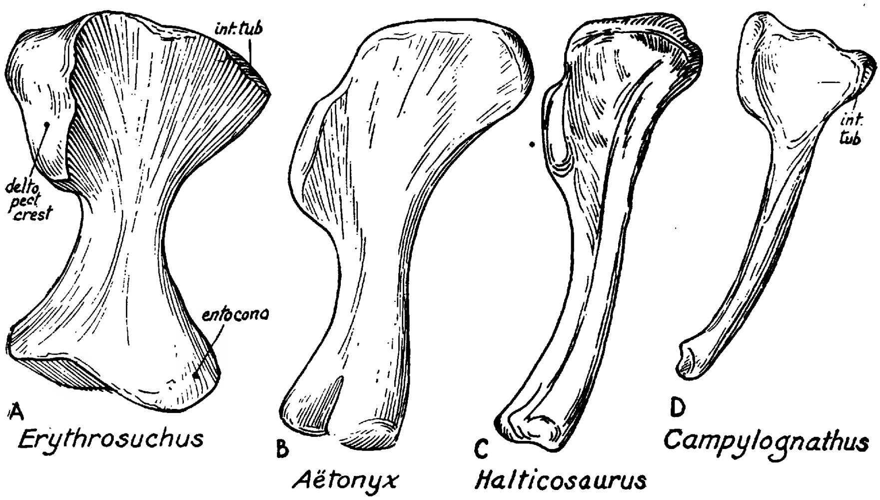


FIG. 14. Structural stages illustrating progressive narrowing of distal end of humerus from relatively primitive Triassic thecodont reptile (A) to Jurassic pterosaur. From Gregory. A, C after von Huene; B after Broom; D from specimen.

ming with the hind limbs have been associated with the use of the stout forearms as springs and shock absorbers, and with the consequent strengthening both of the pectoral girdle and of the shaft of the humerus (fig. 12B). The globular capitellum for the radius permits a wide sweep for the forearm, useful also in swimming and grasping.

These and other modern amphibian types branched off from what we may call the "main line," from fish to man, which passed directly from the primitive tetrapod to the central reptilian humerus (fig. 31).

ADAPTIVE DIVERSITY OF THE HUMERUS IN REPTILES AND BIRDS

The humerus of primitive reptiles (figs. 18A, B, 29A) had advanced beyond the primitive tetrapod humerus in the development of an entepicondylar foramen for the median nerve and ulnar interosseous artery (Huntington, 1918). In many forms the formerly warped trackway for articulation with the scapulocoracoid was shortened into a convex head. The primitive reptilian humerus was fundamentally like the humerus of *Sphenodon* (fig. 31) among modern reptiles, but with much wider proximal and distal ends.

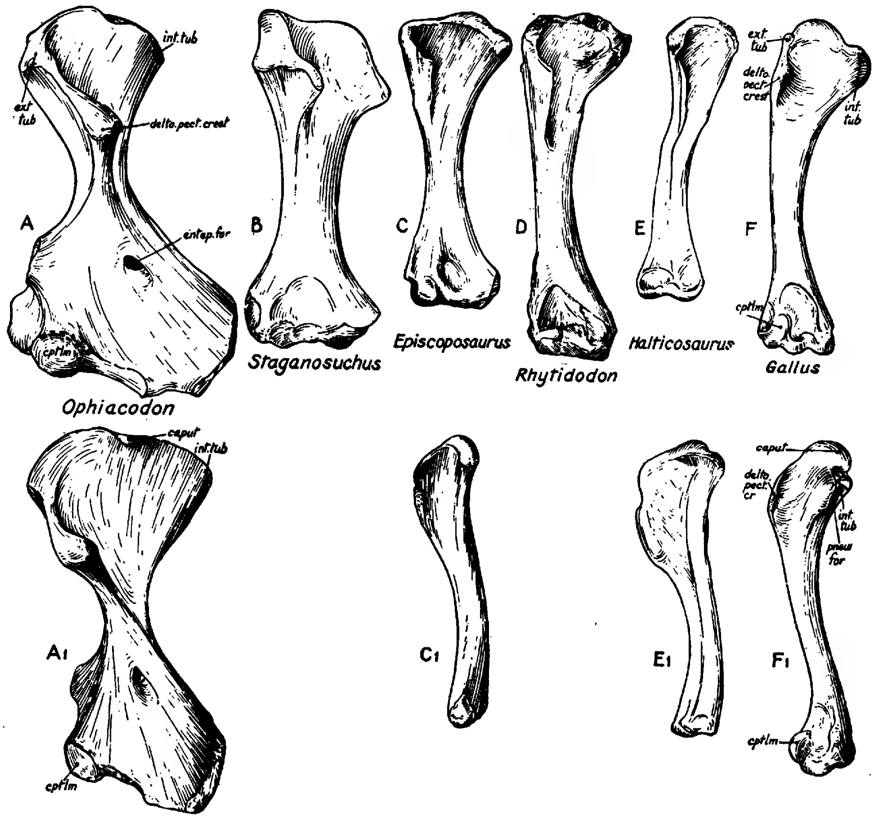


FIG. 15. Ventral (A–F) and medial (A1–F1) views of right humeri. A. Primitive Permo-Carboniferous reptile. B–E. Various Triassic thecodont reptiles. F. Modern fowl. Illustrates progressive lengthening of shaft, reduction of entocondylar process, development and recurvature of convex head. From Gregory. A after Romer and Price; B, C, E after von Huene; D after McGregor; F from specimen.

Such a humerus is adapted primarily for crawling, plantigrade habits, but it has given rise to many specialized forms, some of which may now be briefly noted.

Among the thecodont reptilian stock of Triassic age (fig. 31), which apparently was the source of the aëtosaurs, pelycosimians, crocodilians, dinosaurs, pterosaurs, and birds, the pectoral limbs were often smaller than the pelvic limbs and in the humerus of the smaller, less specialized forms, the convex head (caput humeri) was directed upward and somewhat backward (fig. 15C1). In the modern crocodilians (fig. 31), which are a semi-aquatic side branch

of the lizard-like thecodont stem, the humerus is fairly long and narrow with somewhat sigmoid curve in side view. The entocondylar process, so large in primitive tetrapods, is here represented only by a low convexity for the lateral ligaments of the elbow. The extensor-supinator crest is low and inconspicuous, and the entire distal end forms a transversely placed rounded capitellum-trochlea. This type of humerus compares rather closely with the humeri of relatively primitive saurischian dinosaurs (fig. 31), and Miner's study (1925) of the muscles and muscle areas of tetrapods gives reliable data for interpreting the homologous muscular areas in dinosaur humeri.

Among bipedal, bird-like dinosaurs the humerus and hand were long and narrow; the humerus of *Struthiomimus* had a long, slender shaft, possibly supporting a patagium. In outer side view the humerus was slightly sigmoid, the distal concavity facing forward.

Increasing massiveness of body led on one side from the primitive Triassic thecodonts to the huge, bipedal, flesh-eating dinosaurs, eventually with small hands and short humeri (fig. 31), and on the other to the ponderous, secondarily quadrupedal Sauropoda. The latter had very large humeri with a wide fossa for the thick coraco-brachial muscles, and massive deltopectoral ridge (fig. 31). The distal epiphysis was long-growing and partly cartilaginous. The distal position of the large, radio-ulnar facet permitted a marked opening of the humero-radial angle, useful in walking under water.

The beaked dinosaurs or Ornithischia, which had advanced herbivorous jaws and teeth, were also secondarily quadrupedal and their ungual phalanges bore flat nails. Among them the duck-bill and cassowary-like dinosaurs were semi-aquatic, the fingers partly webbed; their humeri in side view were slightly sigmoid but not notably specialized. In the ponderous quadrupedal ceratopsians, on the other hand, the humeri were very massive (fig. 31) with large proximal crests and sharply bent elbows for the support of the enormous skull. The sharply projecting entocondylar convexity of the early tetrapod humerus had long since been reduced in the small bipedal running ancestors of these huge animals, but with increasing weight the proximal and distal ends of the humerus were secondarily widened and thickened, and the massive distal end was probably tied to the huge ulna and radius by very large and strong ligaments and by thick

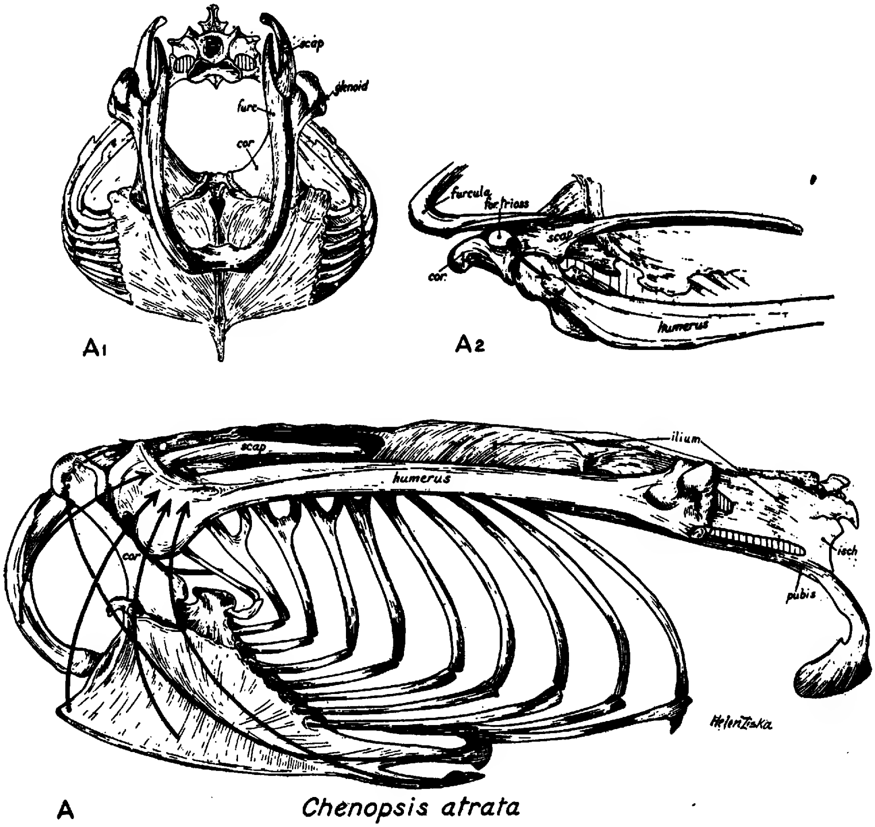


FIG. 16. Humerus, pectoral girdle, and axial skeleton in a bird of strong flight. Showing stiffening of backbone, strong development of sternum, furcula, coracoid, spring-like ribs. The large deltopectoral crest flares out near the proximal end of the columnar humeral shaft. The forward and upward movement of the wing is effected in part by the deep pectoralis minor, the downward movement by the pectoralis major. From specimens.

muscles of great power. Still shorter and relatively wider were the humeri of the armadillo-like ankylosaurs. In brief, humeri of primitive dinosaurs, starting from the small, rather weak humeri of the Triassic thecodonts gave rise to: (1) the very long humerus of *Struthiomimus* with its almost cylindrical shaft and small tuberosities; (2) the long but enormous humeri of certain sauropods (e.g., *Brachiosaurus*); and (3) the extremely massive, wide humeri of the later Ceratopsia and Ankylosauria.

In quadrupeds the length of the humerus is obviously one of the several factors in the length of the stride. The long humerus of

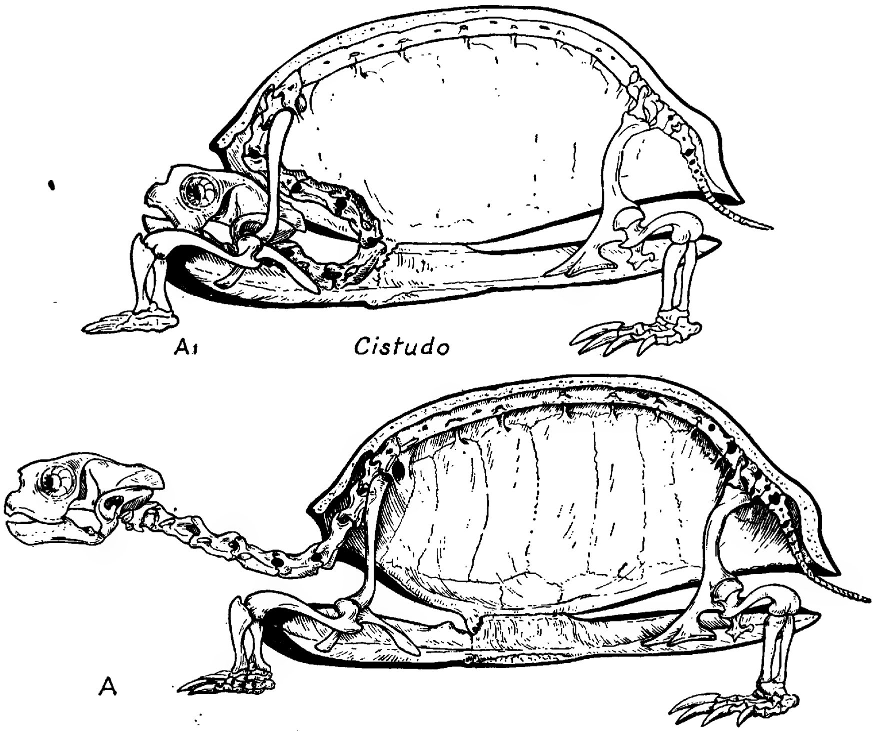


FIG. 17. Skeleton and half section of box tortoise, to show partial enclosure of girdles and limbs by overgrowth of carapace and plastron. From specimens.

climbing animals contributes to the long reach and must withstand relatively great tensile stresses due to weight.

Among the bat-like pterosaurs the shaft of the humerus (fig. 14D, 31) was narrow with thin walls and pneumatic interior. In side view the bone was curved anteroventrally, and there were a high delto-pectoral crest and large coraco-brachialis fossa. The joint at the narrow distal end was more or less hinge-like.

The long humerus (fig. 16) of birds of strong flight has a large oval head facing dorsocaudally, a fairly large internal tuberosity, and a pneumatic interior. Thus the avian humerus, as compared with the central reptilian type, has undergone much less change than has the avian pectoral girdle, in which the sternum has gained a huge base and a high median keel (fig. 16). The humeri of ratite birds is longest in *Rhea* and becomes very small in emus, cassowaries, and *Apteryx*, i.e., as the wings degenerate. The pectoral limb of penguins (fig. 31) has become paddle-like, but

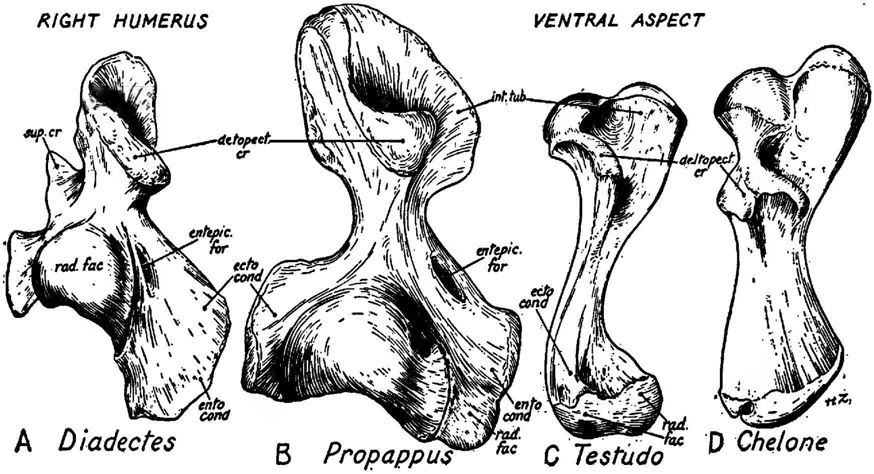


FIG. 18. Comparative series of humeri from primitive reptile (A) to modern sea turtle (D). After Gregory.

the elements of the avian wing are still present, though highly modified (Simpson, 1946).

The marked sigmoid curve of the tortoise humerus (figs. 17, 18), together with the globular, backwardly directed head, permits the humerus to be swung either far forward, so that the elbow looks like a knee (fig. 17), or far backward to enable the pectoral limb to be tucked under the overhanging marginal ridge of the carapace. In spite of its specialization the humerus of the tortoise (fig. 18C) is foreshadowed in basic features by the humerus of pareiasaurs (fig. 18B), which in turn are readily derivable from the primitive tetrapod type retained in diadectid cotylosaurs (fig. 18A). The very peculiar humerus of the sea turtle (fig. 18D) forms part of a pectoral paddle or wing; it is flattened, the distal end widened, the deltopectoral crest much modified, and the medial tuberosity greatly enlarged and flattened.

In ichthyosaurs (fig. 31) the limbs have become completely paddle-like, the humerus was flattened, with wide distal ends, and the rest of the limb has changed into more or less polygonal secondary polyisomeres. The humerus of ichthyosaurs may have been derived from the slender, semi-aquatic humerus of *Mesosaurus*. The humerus of plesiosaurs (fig. 19E, F) is closely connected with that of nothosaurs (fig. 19C) which, in turn, lead backward towards a *Sphenodon*-like type (fig. 19A, B). As in other advanced aquatic reptiles the facet for the ulna is shifted to

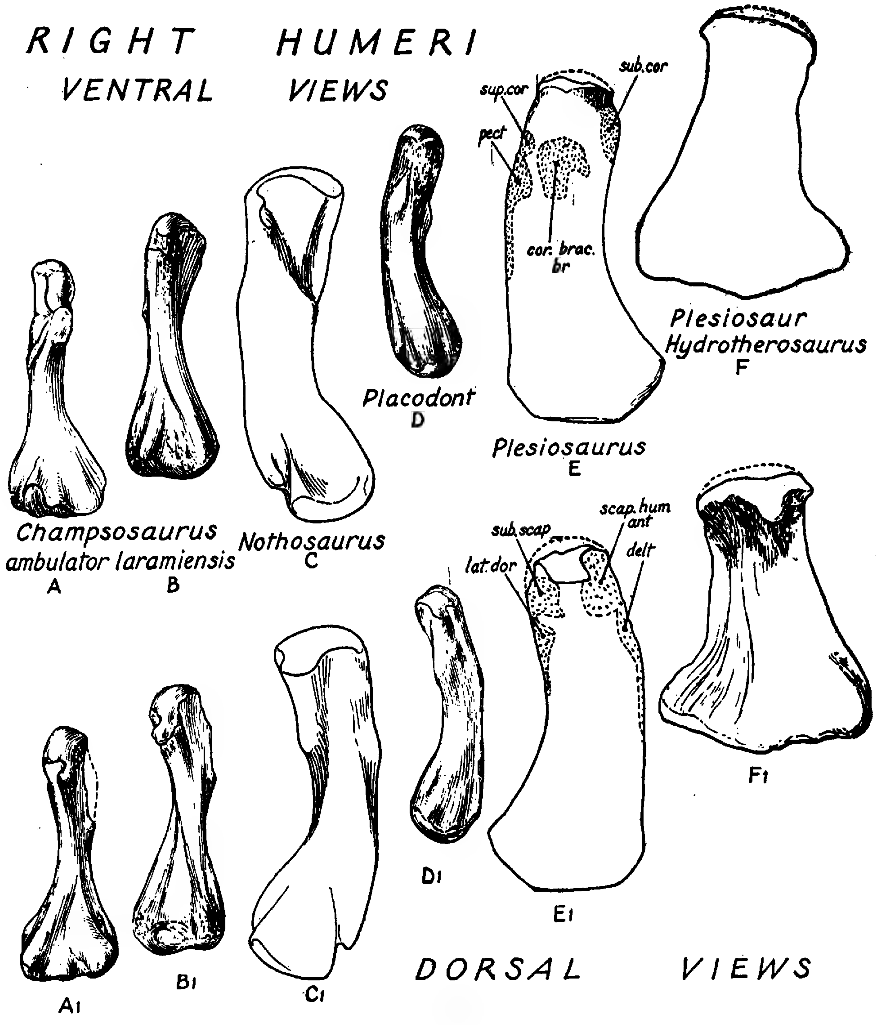


FIG. 19. Comparative series of reptilian humeri; from relatively primitive semi-aquatic form (A, B) to highly specialized marine plesiosaur (F). From Gregory. A, B after Barnum Brown; C, D after von Meyer; E after Watson; F after Wells.

the outer side of the distal end of the humerus so that the olecranal process is lateral to, not behind, the head of the radius, both radius and ulna being flattened into the same plane.

RISE AND DIVERSITY OF THE MAMMALIAN HUMERUS

Returning to the "main line," in the earlier mammal-like reptiles, the humerus of the less specialized pelycosaurs (fig. 29A)

retained a large entocondylar process and was not very different from the primitive tetrapod type in being adapted for a crawling gait. In the giant South African dinocephalians the pectoral girdles and humeri were relatively primitive, although the elbow in standing was less sharply bent and everted than in the primitive tetrapod. For the support of the great body weight the coracobrachialis brevis muscle and its fossa were widely expanded, as well as the areas for the extensors (Romer, 1922, pl. 36). In the gorgonopsians the fairly primitive humerus (fig. 29B), with its moderate sigmoid curve, permitted a somewhat cat-like stride with the body raised well off the ground (Colbert, 1948), with elbows less everted than in primitive tetrapods. In the cynodonts the pectoral girdle approached the mammalian stage especially in the scapula and coracoid, and so also did the humerus (fig. 29C).

Simpson (1928, p. 155) has shown that in the humerus of the cynodont *Diademodon* (fig. 20A) the convex head was directed dorsoposteriorly but was not spherical, and the deltopectoral crest at its proximal end was not yet expanded into a distinct greater tuberosity, although the lesser tuberosity was well developed. A large entepicondylar foramen was retained as well as an ectepicondylar foramen, both being characteristic of reptiles. The deltopectoral crest had begun to be turned medially towards the fossa for the coracobrachialis brevis and biceps muscles.

Among the Tritylodontoidea the humerus (fig. 31) is well shown in *Bienotherium* from the upper Triassic of China (Young, 1947, p. 582). This genus may represent an early side branch of the mammalian Order Multituberculata. Its skull and jaws were advanced beyond the cynodont stage and were almost mammalian. The descriptively multituberculate molars were adapted for crushing hard objects. The humerus closely approaches the primitive mammalian type, but the upper end of the deltoid crest, although it is already raised into a swollen great tuberosity, is continuous with the head, which is not so fully spherical as in typical mammals. There are a large entepicondylar bridge and foramen, and there may be also an ectepicondylar groove.

Among the Jurassic mammals the humerus is known only from three specimens of uncertain ordinal position. As described by Simpson (1928, pp. 155–159) they retained many cynodont features, but in others, such as the nearly spherical head, they were more mammalian (fig. 20B). However, after careful com-

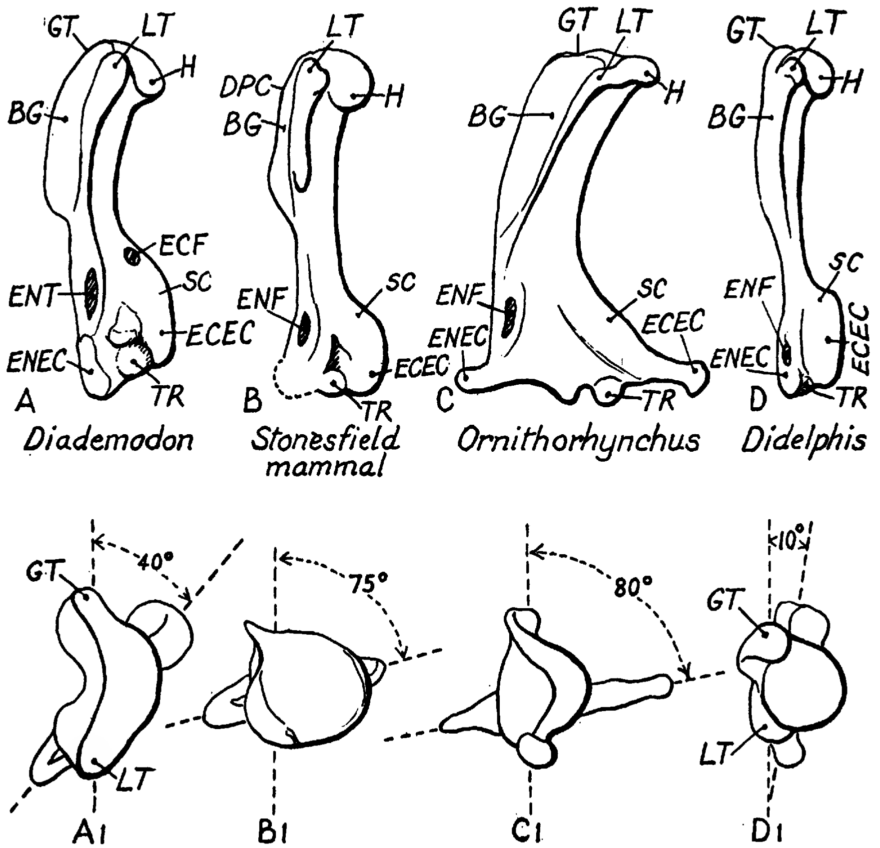


FIG. 20. Median posterior view of right humeri. After Simpson. BG, bicipital groove; DPC, deltopectoral crest; ECEC, ectepicondyle; ECF, ectepicondylar foramen; ENEC, entepicondyle; ENF, entepicondylar foramen; GT, greater tuberosity; H, head; LT, lesser tuberosity; OF, olecranon fossa; SC, supinator crest; TR, trochlea. A1–D1. Proximal views. Not to scale.

parative studies Simpson (*op. cit.*) concludes that these humeri were normally held in a nearly horizontal plane as in cynodonts and monotremes. "The radial and ulnar articulations [of the Stonesfield mammal]," writes Simpson (*op. cit.*, p. 156), "are also extraordinarily reptilian. The true sharp-crested trochlea of later mammals is not well developed. The radius articulates on a separate rounded surface external and somewhat ventral to the ulnar articulation."

The humerus (fig. 20C) of the monotreme *Ornithorhynchus* at first sight recalls that of primitive reptiles, but as Simpson (*op.

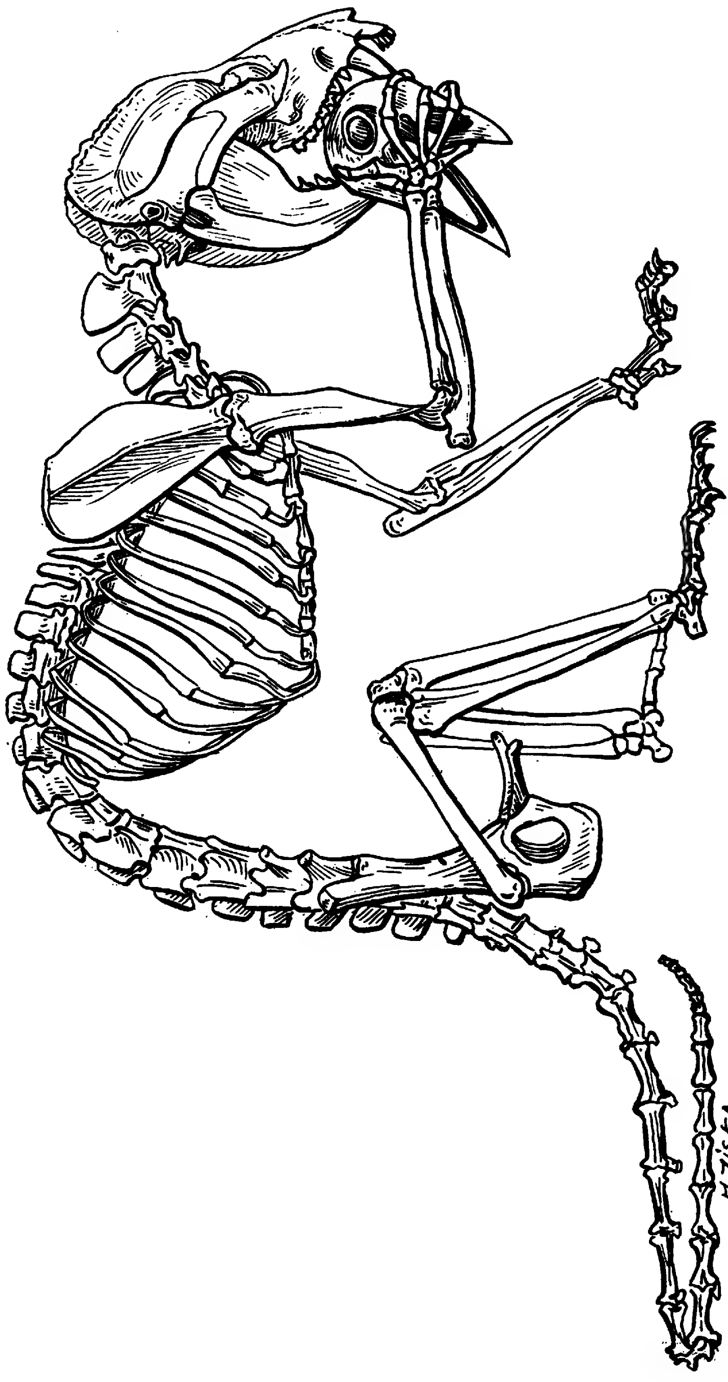


FIG. 21. Skeleton of American opossum, mounted by S. H. Chubb. From Gregory.

cit.) and Howell (1937a) have shown, it is specialized for both digging and swimming. In the pectoral girdle the dorsoposterior border of the scapula is prolonged backward while the prespinous fossa is either vestigial or incipient. The thin, plate-like epicoracoid slides a little on the expanded sternum and strong interclavicle. Although these may be partly habitus features, the girdle of *Ornithorhynchus* as a whole strongly recalls the conditions in *Cynognathus* and indicates that also in the humerus the basic features have been inherited from a remote cynodont ancestor, although the extreme projection of both the entepicondylar and extepicondylar processes (fig. 20C) together with the concavely curved head (fig. 20C1) may be later specializations.

The wide humerus (fig. 22B) of *Tachyglossus* ("*Echidna*") clearly reflects great strength in digging, as do also the block-like coracoid, the well-braced interclavicle, and stout sternum.

According to Simpson (1928, pp. 156–158), in the humerus (fig. 20D) of the opossum *Didelphis* the plane of the distal end diverges only about 10 degrees from that of the proximal end (drawn through the greater and lesser tuberosities), whereas in the Stonesfield humerus (fig. 20B1) of a Jurassic mammal the corresponding angle is about 75 degrees and in *Diademodon* only 40 degrees. This accords with much other evidence that, as we pass from early tetrapods to mammals, the angle between the proximal and distal ends of the humerus approaches zero. This is no doubt associated with the drawing inward of the elbows and opening of the angle at the elbow as in typical mammals.

The humerus of *Didelphis* (figs. 21, 22) also is typically mammalian in possessing a distinct lateral or greater tuberosity on top of the deltoid crest. Upon it are inserted both the supraspinatus and infraspinatus muscles, which are pretty certainly derived from the supracoracoscapula muscles of reptiles (Romer, 1922, p. 594). Likewise an internal or medial tuberosity was present, to which was attached the subscapularis muscle. The "mammalian" posture of the humeri of *Didelphis*, with the elbow almost immediately beneath the caput humeri, is made possible not only by the various mammalian features of the humerus itself, but (1) by the freeing of the reduced coracoid from direct contact with the sternum, (2) by the wide mobility of the whole complex of clavicle, coracoid, acromion, scapula, and humerus around the sternal articulation of the clavicle, and (3) by the protection afforded to the shoulder joint by the overhanging acromion and its ligaments.

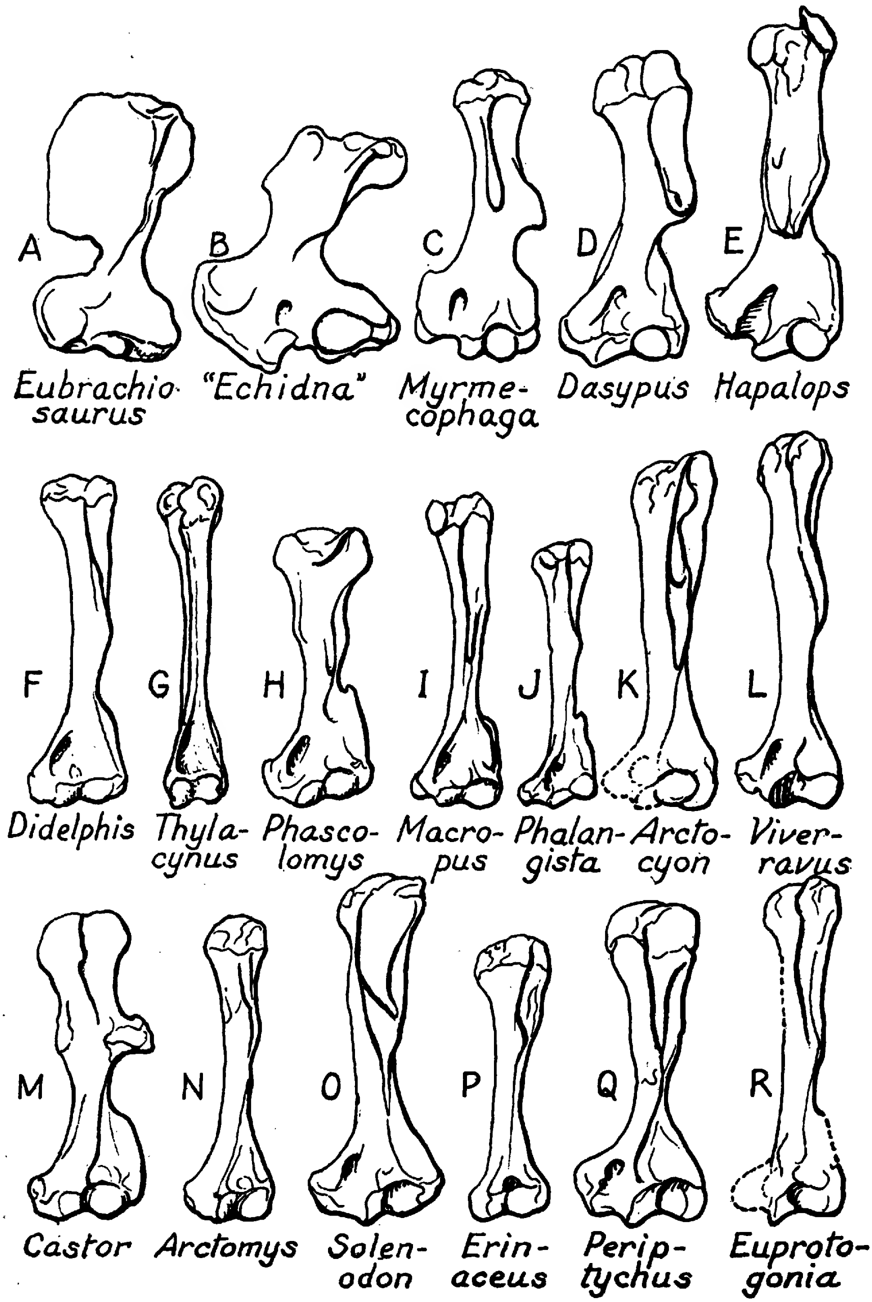


FIG. 22. Left humeri of various primitive and adaptive types. From Gregory. A after Williston; E after Scott; others from the American Museum of Natural History collections.

Doubtless the moving outward of the shoulder joint away from the midline exposed it to greater danger from breakage in falling, but the resulting mobility, the wider reach and swing of the fore-limb, contributed much to the increased speed, effectiveness, and endurance of mammalian over reptilian locomotion. The *Didelphis* pattern of pectoral girdle and humerus appears to be archetypical to that of all other marsupials.

In the "marsupial wolf" (*Thylacynus*) the marked elongation of the humerus (fig. 22) has helped to lengthen the stride of this cursorial predator. The entepicondylar and ectepicondylar projections were much reduced. The distal facet indicates a chiefly hinge-like movement at the elbow, with limited supination.

At the other adaptive extreme, in the humerus of the "marsupial mole" (*Notoryctes*), digging powers are indicated by the marked widening of the distal end, by the strength of the crests, and by the winding surface for the brachioradialis.

Among the diprotodont marsupials the phalanger humerus (fig. 22J, *Phalangista*) is close to the didelphid type, but with some increase of the supinator-extensor crest. The humerus (fig. 22) of the wombat (*Phascolomys*), a powerful digger, is evidently derived from the phalanger type, but it has become stouter, distally wider, with projecting tuberosities and crests. On the whole there is a certain convergent resemblance to the cynodont humerus (fig. 29C), but the head is more spherical and the distal end completely mammalian.

The humerus (fig. 23) of the giant herbivorous *Diprotodon* and related genera is associated with a very peculiar form of scapula in which there is a large, cap-like, dorsal protuberance directly above the vertical scapular spine. To this may have been attached a thick dorsoscapular ligament, while below it was the serratus anterior muscle, supporting the massive body. The vertebral border of the scapula is extended far downward, and the axial margin is greatly reduced. The inferior angle ends in a prominent, downwardly projecting tuberosity, possibly for a robust teres minor. Perhaps in correlation with these and other features the ulna has an enormous, transversely widened olecranon for the triceps, and the middle of the lateral aspect of the humerus bears a prominent, laterally projecting process and rugosity, probably for the deltoid muscle. In short the humerus of *Diprotodon* as compared with the primitive phalanger type, in becoming gigantic and graviportal, has on the whole been simplified.

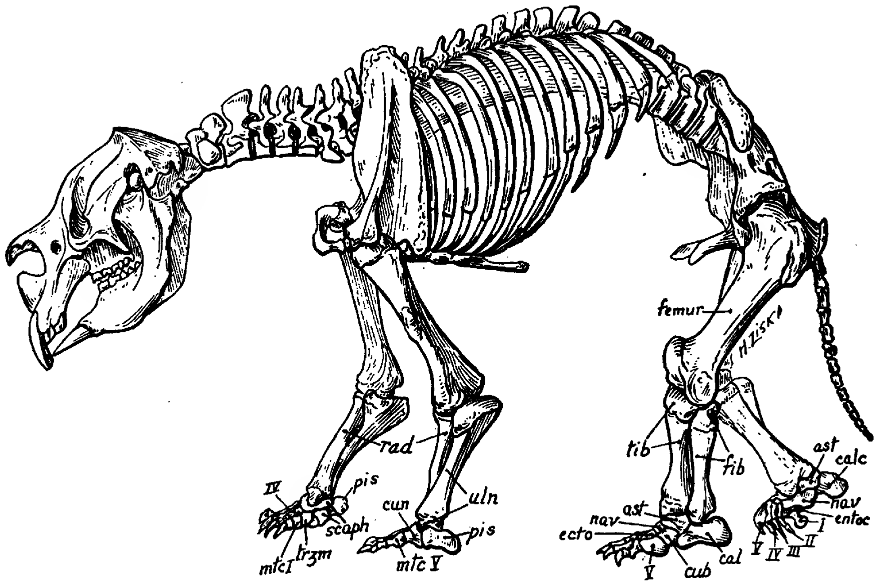


FIG. 23. Skeleton of *Diprotodon*. From Gregory.

Among the placental mammals adaptive branching was already prolific in the Paleocene and Lower Eocene epochs, and there were many lines that subsequently became extinct as well as a few that branched in later times. Matthew (1904, 1937) showed that the known hands and feet of Paleocene and early Eocene placental families were pentadactylate, with spreading digits and partly divergent pollex and hallux, respectively, also that the radius and ulna could be freely supinated. He regarded these and correlative characteristics of the girdles, limbs, and vertebrae as indicating for the placental mammals arboreal ancestry, as already had been held to be so in marsupials by Dollo (1899) and by Bensley (1901).

The humeri of the smaller Paleocene and Lower Eocene placental mammals, so far as known, were of the same basic pattern as the opossum humerus (fig. 22F), but the extensor-supinator crest (fig. 22K, L, O) was less flaring at the upper or proximal end. It sloped evenly towards the shaft of the bone and did not end above in a sharp notch. At the distal end the capitellum is less spherical in front view than it is in *Didelphis* (fig. 22F), and the trochlea often has a sharp inner keel extending distally below the level of the capitellum. In the living *Gymnura* (fig. 31), a fairly primitive

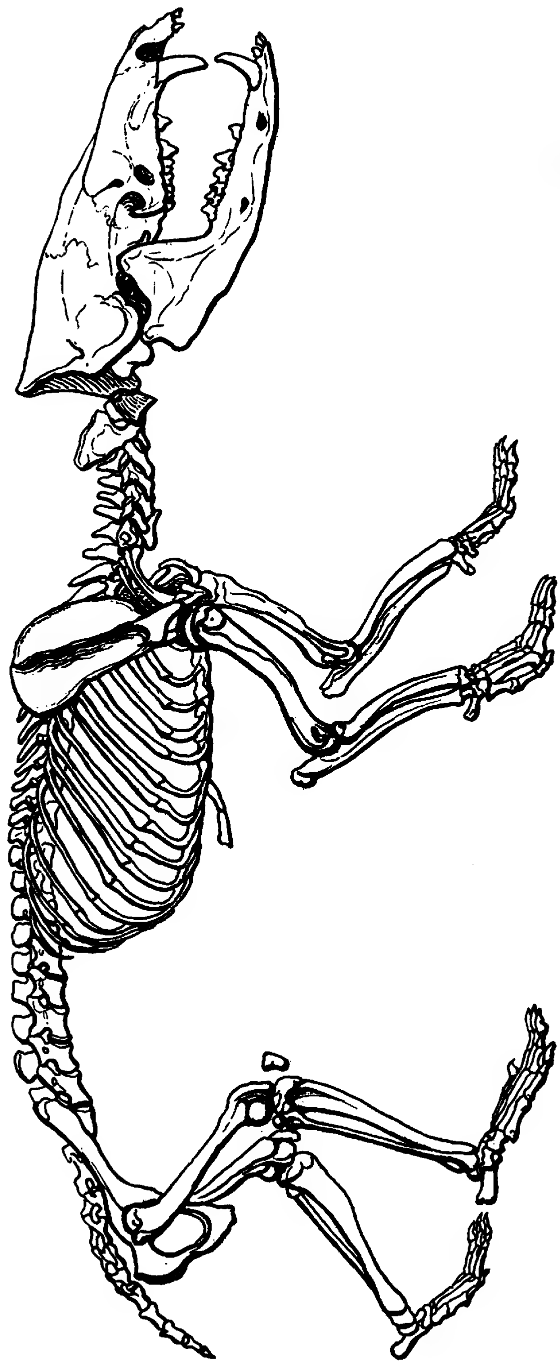


FIG. 24. Skeleton of placental insectivore *Centetes*. From Gregory, after De Blainville.

insectivore, as well as in *Centetes* (fig. 24), this kind of elbow joint is associated with a transverse widening of the head of the radius, which extends across to, and even a little beyond, the inner keel of the trochlea. With such a joint only a moderate supination of the radius is possible, and this condition predominates among both fast running and digging mammals. And among the primitive Paleocene and Lower Eocene placentals (except possibly *Nothodectes*) there is little or no suggestion of the "outer lip" of the trochlea (figs. 25, 28) which is developed in arboreal Primates (Gregory, 1920, p. 71; Simpson, 1935, p. 13).

A review of the skeletons of Paleocene and Lower Eocene mammals suggests that these early placentals were nearer to ground-living, unguiculate, semi-fossorial ancestors than they were to a more remote arboreal stock (fig. 31). Advanced fossorial habitus was already attained in the mole-like Paleocene humerus (fig. 31) described by Simpson (1937, p. 140). This further indicates a fairly long antecedent history of partly ground-living habits for the placentals, extending well back into the Upper Cretaceous. As noted above the only known mammalian humeri of the Triassic (fig. 31) and Jurassic (fig. 20B) ages tend to connect the marsupials with the cynodont stock, and the detailed characters of the Stonesfield humerus indicate normally horizontal posture with elbows widely everted (Simpson, 1928). Such a combination may have been useful in a partly climbing, partly digging, ambulatory stage, ancestral to the known diversified Paleocene humeri.

With increasing speed and lengthening stride the humerus may become either relatively long and narrow as in the dog (fig. 31), or short and thick (when the power is concentrated in the proximal segment) as in the horse (fig. 31) and other fast cursorial herbivores. The elbow joint also becomes quite hinge-like, and the movement is limited to extension and flexion. Especially in massive, heavy-bodied mammals, the entocondylar eminence is often pronounced, indicating very strong ligaments. The deltopectoral crest is usually prominent, and so also are the winding surface for the brachialis inferior muscle and the extensor-supinator crest.

In heavy-bodied ungulates which have large scapulae and heavy shoulder muscles the great tuberosity of the humerus sometimes becomes very large and high, especially in elephants, titanotheres, and horses (fig. 31).

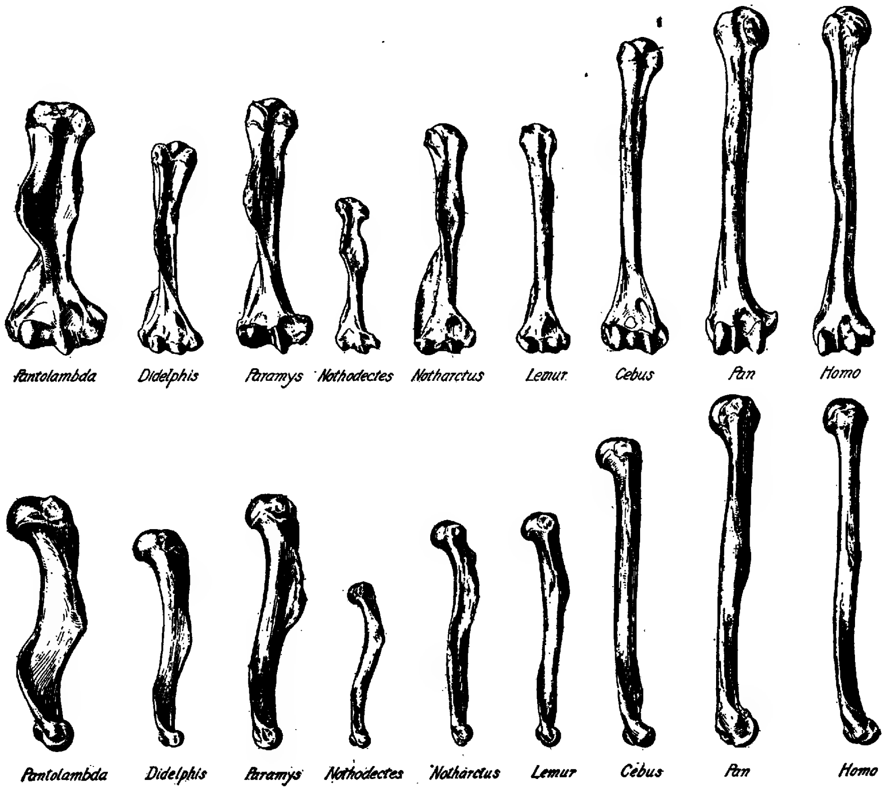


FIG. 25. Humeri of primitive placental mammals and primates. After Gregory.

In digging types, the more or less sigmoid curve of the humerus, as seen from either side (fig. 25), is probably associated in part with a markedly spiral brachialis channel, but it may also serve to shorten the humerus, thus lessening adverse leverage and making it easier to turn around in a narrow tunnel. This sigmoid flexure is also pronounced in swimmers such as otters and seals.

The somewhat sigmoid humerus of the manatee and other sirenians is short, with pronounced deltopectoral crest. The elbow joint is rather hinge-like. The whole bone is excessively dense and heavy as are also the ribs.

In cetaceans, whose entire pectoral limb has been changed into a flipper, the humerus, radius, and ulna are flattened, the humerus is distally widened, while the phalanges are multiplied, recalling the conditions in pleisiosaurs. Among the most specialized

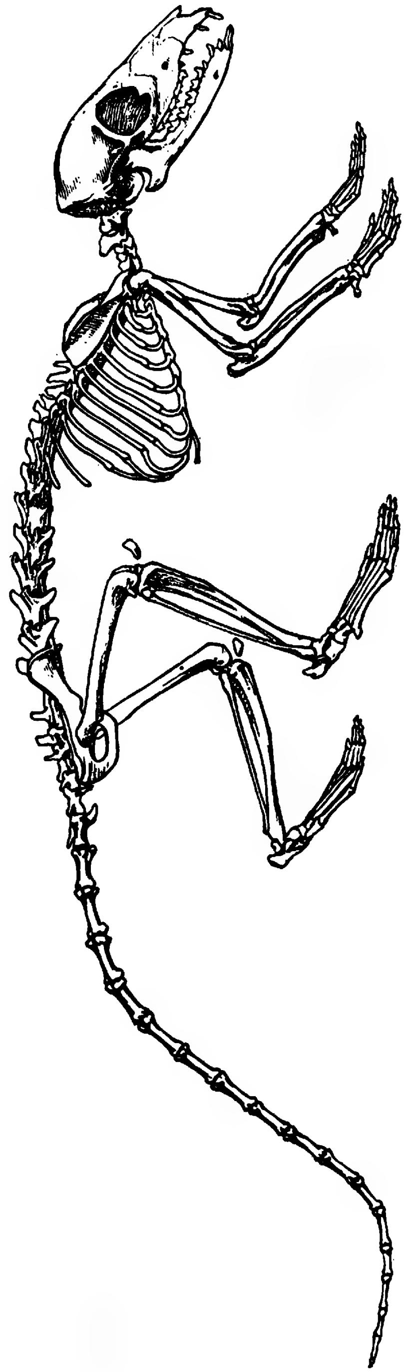


FIG. 26. Skeleton of tree shrew (*Tupaia*). From Gregory, after De Blainville.

cetacean humeri is the humerus of *Eubalaena* (fig. 31) with extremely short shaft, huge spherical head, wide distal end, and small antero-internal tuberosity, possibly for the mastohumeralis muscle (cf. Schulte, 1916).

The very long, somewhat cylindrical humeri of "flying lemurs" (cobegos) are sufficiently strong to resist the bending moments imposed by the weight of the body in skimming through the air and landing, and by the pulls of the long extensors and flexors. The cylindrical radius is much larger than the splint-like ulna which is coalesced distally with the radius. Thus the movement at the elbow is largely hinge-like, as indicated also by the widened head of the radius. In the fruit bats, the humerus (fig. 31) is also very long and slender. In the Microchiroptera two processes, one on either side of the head of the humerus, sometimes articulate with the scapulo-coracoid, thus limiting the movement, but increasing the strength, of the joint (Miller, 1907). Doubtless the associated ligaments must be relatively strong.

THE HUMERUS FROM TREE SHREW TO MAN

The Recent and extinct "tree shrews" (Tupaioidea) although long classed with the Insectivora agree with or approach the lemurs in many significant structural features (cf. Gregory, 1910, pp. 269–285) and have been transferred to the lemuroid primates by recent authors (cf. Simpson, 1945, pp. 61, 176). In the Recent *Tupaia* the humerus (figs. 26, 32) and the forearm are both long and slender, and the radius is about as long as the humerus. The head of the humerus is large and spherical, the great tuberosity low, and so is the deltoid crest. The bicipital groove is barely indicated, the extensor-supinator crest small, an entepicondylar foramen is present. The entocondylar eminence is conspicuous, indicating thick tendons of the pronator and flexor muscles. The capitellum is relatively large and globular, the head of the radius subcircular on the medial side. The trochlea is relatively small and, except perhaps in extreme flexure, the small coronoid process of the ulna seems to have little share in the front face of the trochlea, which in the front view is in contact solely with the radius. Nevertheless, moderate, though not extreme, supination seems possible, as is indicated by the short, spreading hands with compressed, curved, pointed claws and well-developed, partly divergent pollex.

All these and other features may be preadaptations for arboreal

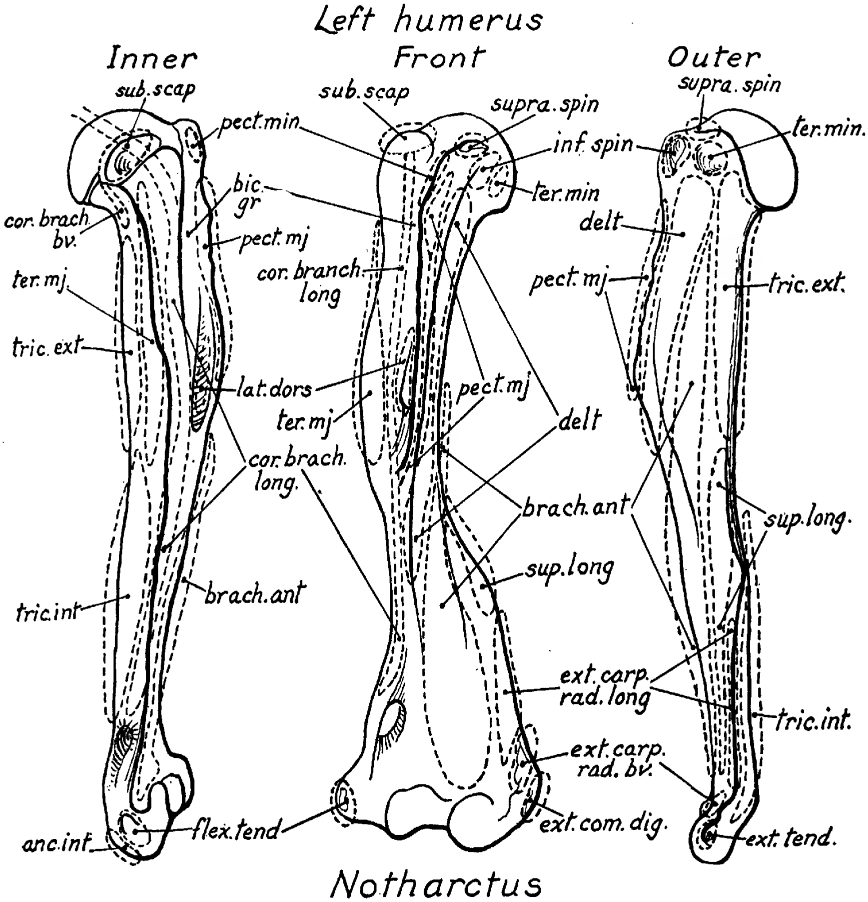


FIG. 27. Humerus of *Notharctus* with muscle areas inferred from those of recent lemurs. After Gregory.

life rather than completed arboreal adaptations, especially since but few of the numerous species of tree shrews are truly arboreal, most of them apparently living on the ground among the roots of trees or on low bushes (Lyon, 1913, p. 21). But there is no doubt that certain species (*ibid.*, p. 57), and especially the pen-tailed tree shrew (*Ptilocercus lowi*) of Borneo, are arboreal.

The Paleocene family of Plesiadapidae, long regarded as a member of the Order Insectivora, was referred to the tree shrew group by Matthew (1915). The humerus (fig. 25) of "*Nothodectes*" (= *Plesiadapis*) seems indeed to afford a structural stage

leading from semi-terrestrial to the fully arboreal habitus of the Eocene and Recent lemuroids. The humerus of *Nothodectes* was relatively shorter and wider distally than that of *Ptilocercus* (Gregory, 1920, p. 70, pl. 27), and its more strongly developed crests and process suggest a stronger, probably ground-living type. Simpson (1935) during a careful analysis of the morphological characters of the *Plesiadapis* ("*Nothodectes*") skull, dentition, vertebrae, scapula, humerus, radius, etc., referred the Tupaioidea, including *Plesiadapis* and the tree shrews, to the Suborder Lemuroidea.

In *Notharctus*, a quite primitive Eocene lemur, the humerus (fig. 25) somewhat resembles the climbing opossum type (figs. 21, 22) especially in its large extensor-supinator crest (fig. 27). But the opossum has a relatively short, well-clawed hand and comparatively strong flexor muscles, whereas in *Notharctus* the whole arm and hand was long and slender, with thin fingers and weak flexors of the digits; it also had nails, not claws. Here, as in many other cases, two mammals with very different kinds of hands, conforming to different locomotor habits, may have less distinctly dissimilar humeri.

The *Notharctus* type of humerus (figs. 25, 28) was evidently well fitted to give rise by minor successive changes to the diverse humeri of later lemuroids and monkeys and eventually to those of apes and man. The humerus of *Tarsius* appears to be a specialized derivative of the *Plesiadapis-Notharctus* stem (Gregory, 1920, p. 75).

The humeri of New World monkeys (fig. 28) often retain an entepicondylar foramen, but their shafts are thinner than in *Notharctus*, and the supinator crest is less flaring distally. The "outer lip" (fig. 25) or ridge of the trochlea, which is beginning in *Notharctus*, is better developed in the New World monkeys and in all higher types, culminating in the anthropoids and man (fig. 28). Its presence marks the increase in width of the coronoid process of the ulna (fig. 33) which now supports the medial part of the circular radial head and takes up a part of the trochlea which was formerly (in Paleocene mammals) occupied by the medial part of the transversely oval head of the radius. This arrangement permits extreme supination and greatly strengthens the flexor side of the elbow joint.

The humerus of the macaque (fig. 28), a fairly central Old World monkey, is more or less intermediate between the lemuroid

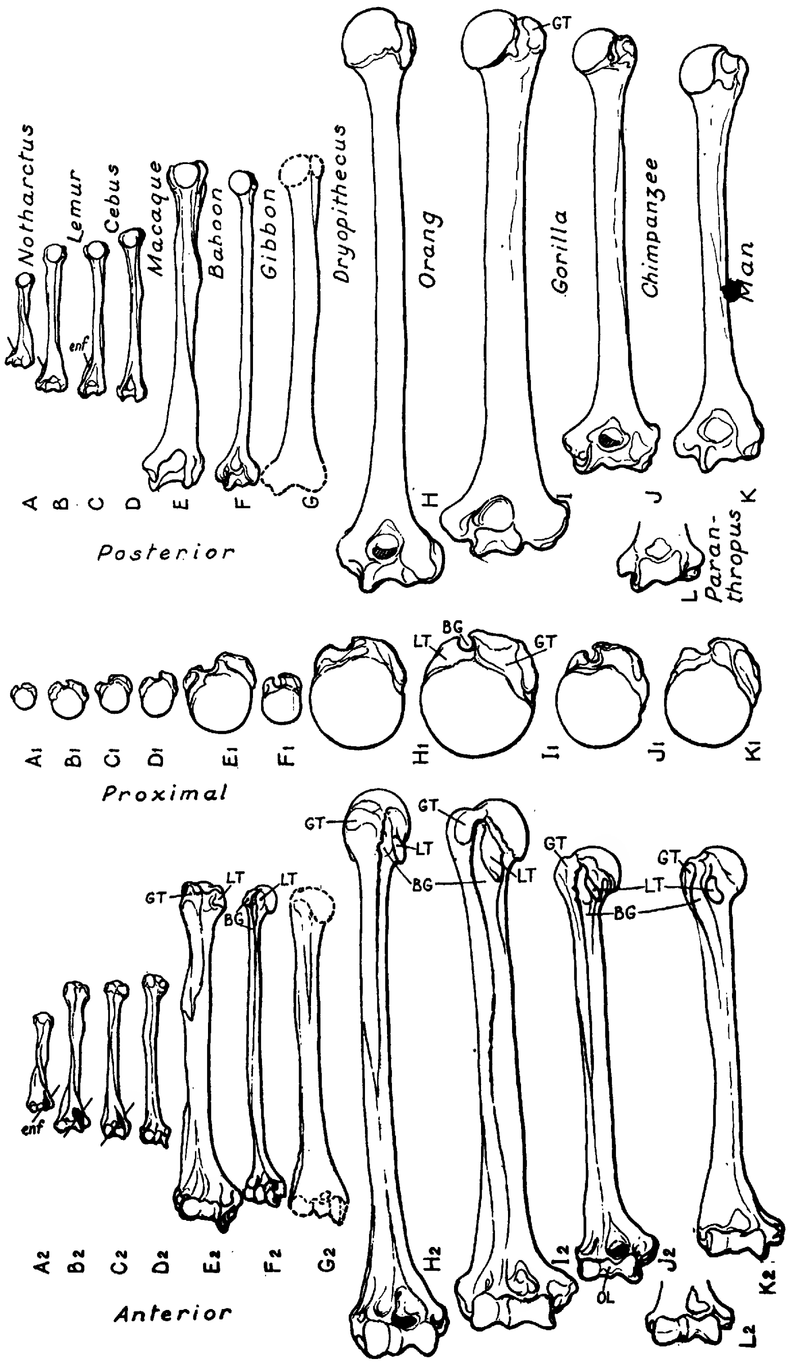


FIG. 28. Humeri of monkeys, anthropoid apes, and man. After Gregory.

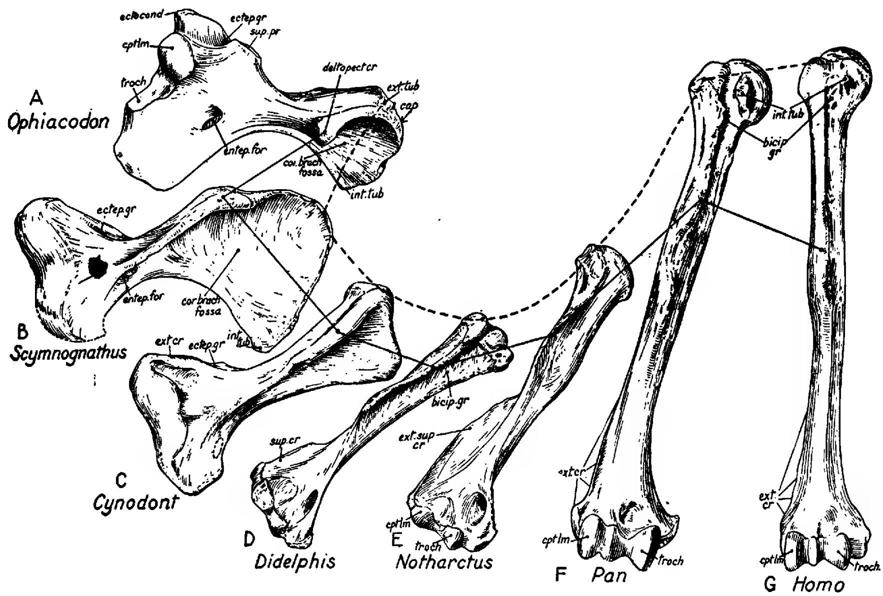


FIG. 29. Anterior aspect of the right humerus, in standing pose; structural series, from primitive mammal-like reptile to man. From Gregory. A after Romer and Price; B after Broili and Schröder; C–G from specimens.

and anthropoid types. The gibbons (fig. 28) with their extremely long arms and fully brachiating habits are often regarded as irrevocably specialized side lines (Howell and Straus, 1931). But this conclusion takes for granted the dogma of irreversibility and disregards the principle of correlated changes in structure and function. The humerus of the orang (fig. 28) looks almost as if it were a gigantic gibbon humerus. The fossil humerus referred to the Miocene *Dryopithecus* (fig. 28) combines features of the gibbon and of the modern great apes (Gregory, 1928; Ehrenberg, 1938).

The apes all have the ability to swing the arm around the shoulder joint, and describe a very low cone or almost a circle. The human arm has lost little if any of this ability, and the whole shoulder girdle and arm and hand of man (fig. 33) differ from those of the chimpanzee and gorilla only in the proportional emphasis of certain parts, as of the thumb in man or the great width of the hand in old male gorillas.

The distal end of a humerus (fig. 28) found by Broom at Kromdrai near the site of the *Paranthropus* type skull is confidently re-

ferred by Broom to that genus. In other features (e.g., jaws and teeth) the Australopithecinae present a mixture of ape-like and human features, and it is not surprising to find more or less mixed or generalized features in the humerus. But even if we set this specimen aside for the present, the humeri (fig. 28) of chimpanzees and gorillas differ from those of man chiefly in rather small proportional measurements.

RETROSPECT

Man has inherited from the earliest vertebrates, exemplified by the Silurian ostracoderms (fig. 1), the basic pattern of locomotion based upon bilaterally arranged myomeres on either side of an elastic axis and directed by a nervous system of primitive fish type. Man also owes to the ostracoderm grade the outgrowth of pectoral buds from the lateral myomeres and the beginnings of a pectoral girdle. To the same or some related group of pre-fishes, man owes the elaboration of bony tissue with its high adaptability in growth and plasticity in evolution.

Man owes to the crossopterygians (fig. 9) of early Devonian age, the modelling of the proximal metapterygial piece into a potential humerus, and of the second metapterygial piece into a potential ulna. The radius appears to be represented by the first pre-axial radial rod.

The many-jointed pectoral paddle of *Eusthenopteron* (fig. 6) and *Sauripterus* (fig. 31) was evidently quite flexible, the flexibility increasing towards the periphery. When such a fish paddle was transformed into a primitive tetrapod limb the widening of the head of the humerus (fig. 11) limited its mobility to a rocking and twisting movement of the shoulder, within the limits imposed by a rather narrow and warped articular surface and doubtless also by the capsular and associated ligaments. Especially in tetrapods further restraining and strengthening reactions were exerted by the acromial and coracoid processes (figs. 21, 23, 24, 26, and 32) and their ligaments surrounding the head of the humerus. The clavicle, on the one hand, transmitted to the sternum medially directed thrusts of the humerus, and, on the other hand, by being tied to the sternum medially and to the acromion laterally, the clavicle helped to prevent the humerus from being pulled too far away from the sternum. At the other extreme, in some specialized cursorial mammals (fig. 31, horse) the loss of the clavicles is compensated, and part of the weight of

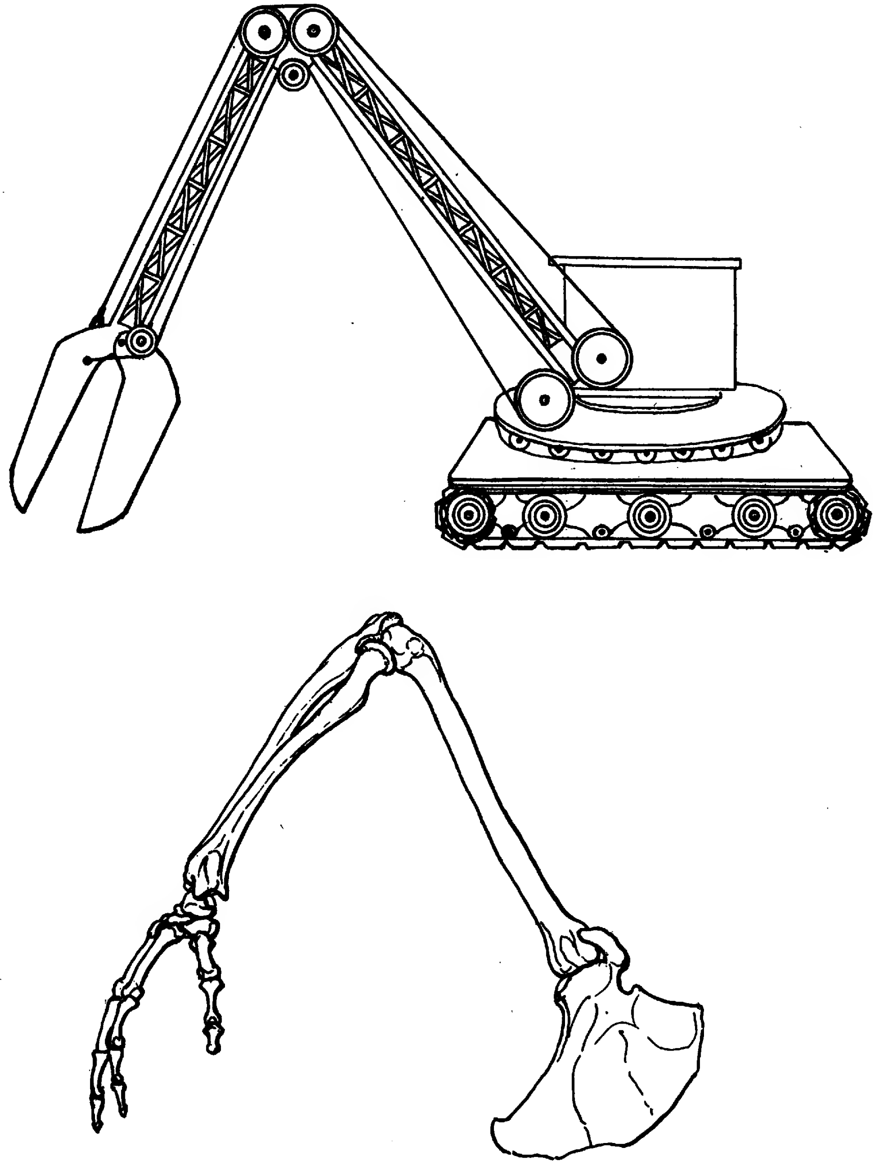


FIG. 30. The human arm and hand, conceived as a modified derrick and manual organ.

the thorax is supported, by the dorso-scapular ligament (Schmaltz, 1905) which permits a wide fore-and-aft swing of the scapula and humerus and lessens the danger of dislocation of the shoulder.

To the earliest tetrapod stage (figs. 9, 13), typified by the Upper Devonian, Carboniferous, and Permian labyrinthodonts, we owe the third major stage in the evolution of the pectoral girdle and limbs. At that time the bend at the elbow was sharply emphasized (fig. 13). Both ends of the humerus were wide (fig. 11), the very short shaft was strongly twisted (fig. 12), the entocondyle and ectocondyle, the extensor-supinator and deltopectoral crests were very prominent, while the articular surface at the head of the humeri formed a long, warped trackway (fig. 11). These features were profoundly modified or sacrificed in later stages, but they were nevertheless prerequisite for further advance. For our ancestors had to swim before they could crawl, to crawl before they could run, to run on the ground before they could climb and leap among the trees, to brachiate, at least to some extent, before they could walk upright on the ground.

To recapitulate, in general, primitive tetrapod humeri in both amphibians and reptiles were short and wide, with very wide distal ends for powerful flexors and extensors of the elbow. The large capitellum for the radius was chiefly ventral rather than distal in position, the elbows being sharply bent. The "head" or proximal articular facet was narrow, not spherical, and directed upward and inward rather than upward and backward. In modern urodele amphibians the proximal and distal ends of the humerus often become cartilaginous. Among later quadrupedal reptiles, the bent-limbed type of humerus was retained in lizards and *Sphenodon;* but the head (caput humeri) has thickened, and in the tortoise it became spherical.

When the length of the stride increases, as in crocodilians, the humeral shaft becomes longer and narrower, the entocondylar and ectocondylar processes disappear, and the elbow joint becomes more hinge-like. In side view such humeri are somewhat sigmoid. In the smaller pterosaurs, the shaft of the humerus was slender, but the deltopectoral crest remained large. In the largest pterosaurs, the humerus (fig. 31) is relatively short in comparison with the very long wing, supported by the enlarged fourth digit. By somewhat parallel changes the primitive thecodont humerus gave rise to the slender and light but strongly built bird humerus (fig. 31). At the opposite extreme in the aquatic icthyosaurs the humerus retained the wide distal end but was flattened to support the paddle-like forearm and hand.

In the line leading towards the mammals (fig. 31), the head be-

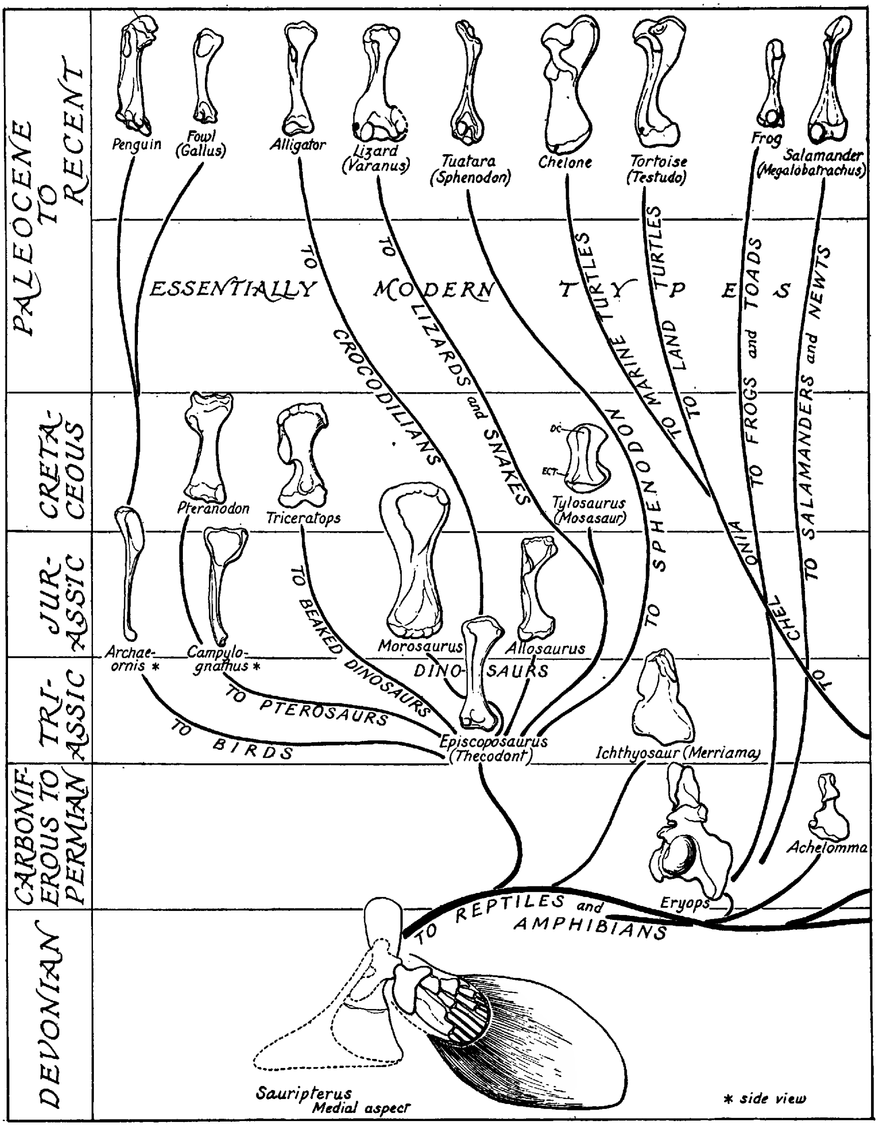
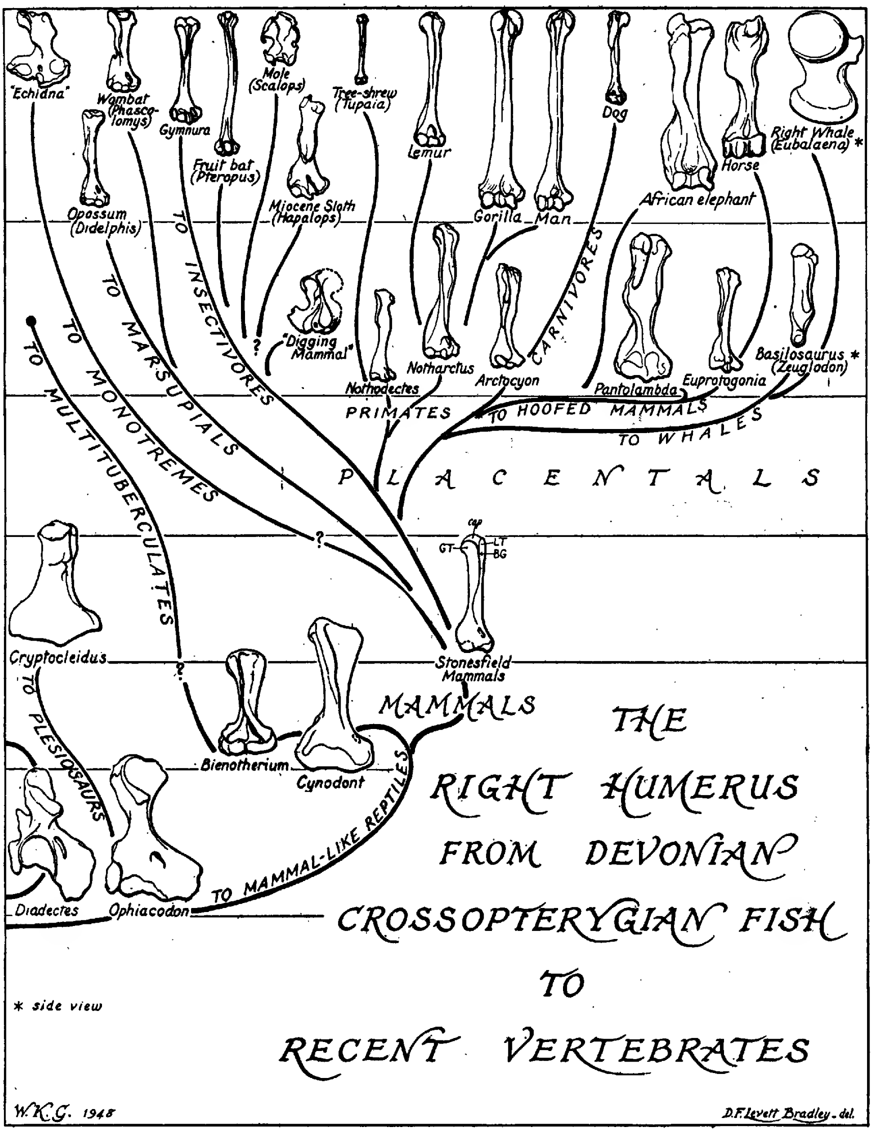


FIG. 31 (THIS PAGE AND OPPOSITE). Adaptive and phylogenetic evolution of the humerus in vertebrates.

came more spherical and directed backward, and the greater tuberosity developed on top of the deltoid crest. As the head withdraws dorsoposteriorly the deltopectoral crest, its greater tuberosity, and the lesser or medial tuberosity tended to define a



bicipital groove. In digging forms the humerus became secondarily widened and shortened, with extreme emphasis of the entocondylar and ectocondylar processes. Advanced aquatic specialization resulted in convergence towards the marine reptiles (fig. 31). At the other extreme, in the fruit bat, the shaft became very long and cylindrical. Among fast-running ungulates (fig. 31) the

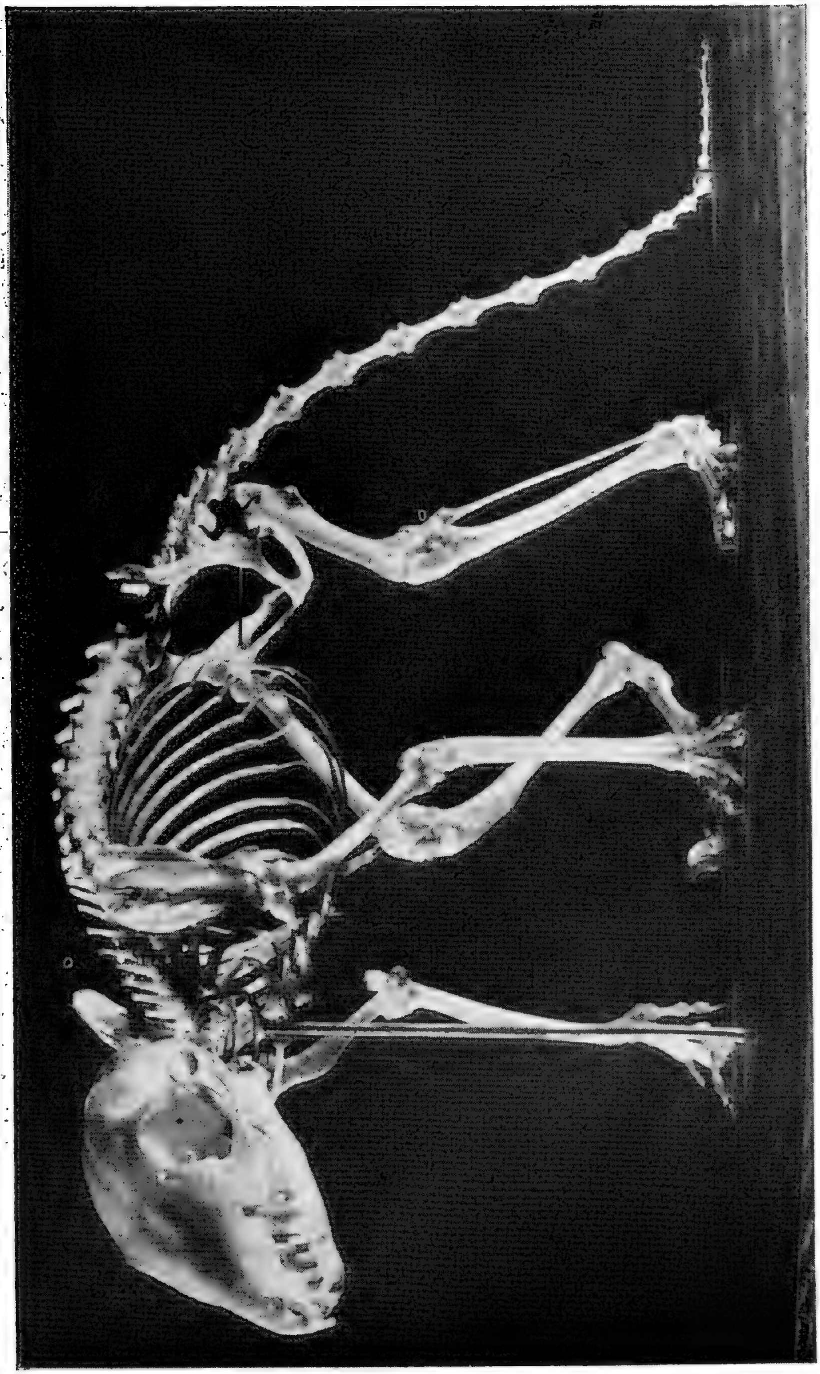


FIG. 32. Mounted skeleton of tree shrew, *Tupaia* sp.

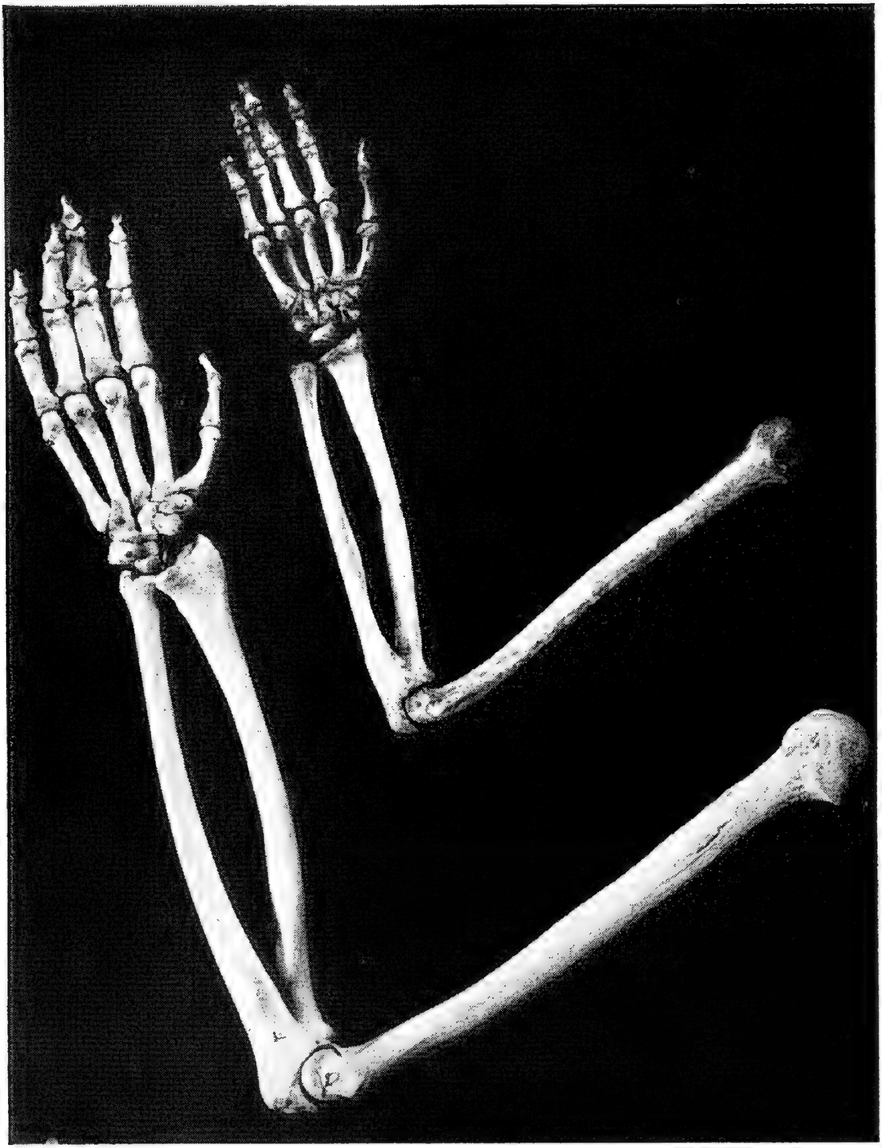


FIG. 33. Right pectoral limb skeleton of man and gorilla. Medial view of humerus and forearm, palmar view of wrist and hand.

humerus is shortened and thickened, the elbow sharply bent and restricted to hinge-like movement.

The foregoing brief review has bearing on several classic problems that are still of daily importance to the student of evolu-

tion. The humerus in life is of course an indispensable part of a continuous, organized whole. In the dried skeleton it appears to be distinct from its neighbors because we do not usually see the joints and ligaments which connect it with its fellows and set limits to its movements, nor the opposing sets of the muscles which operate it, nor the endlessly complex nervous organization which moves and checks it purposively and requires of it sufficient quickness, precision, and power as a condition of its owner's survival.

In man as in other mammals the entire pectoral girdle and appendages serve as a system of compound extensible levers used in locomotion (fig. 24) and, by change of function, as an organ of prehension (fig. 21, 26, 30). As an organ of prehension and manipulation man's pectoral limbs (fig. 30) comprise on either side a modified derrick-crane with a movable base (the shoulder girdle), and a boom, the humerus. The latter supports at the elbow joint a secondary boom, the ulna and radius. This segment can be extended, flexed, and rotated. The wrist and hand (fig. 33) together form a third segment with a compound base (the wrist), and five jointed booms, the metacarpals and digits. Individually these act like little derricks, but collectively they serve as an organ for grasping, pulling, picking, hitting, batting, punching, twisting, throwing, drumming, piano-playing, violin playing, drawing, writing, gesturing, or what you will. In every one of these the humerus plays its part like a well-trained member of an orchestra.

The so-called mystery of adaptation, in the humerus as elsewhere, appears to be due partly to the very human habit of looking at only one finished product and imagining that it was "designed" first and made afterward. But the present sketch suggests (fig. 28) that the human humerus has evolved out of a primitive ape humerus, and the ape humerus from a macaque-like humerus, that in turn from a lemuroid stage, and so on back to *Eusthenopteron* and beyond that. Each earlier stage was attained by change of emphasis or proportion of certain still earlier parts and by correlated loss or increase in dimension of other earlier parts; also each and every earlier stage was prerequisite to all its derivatives. Such a system is operated according to geneticists by the testing of relative survival value in humeri of varying characteristics. The chance encounter of a given humerus type with fortuitously developed new opportunities has made possible every

"creative," "emergent" type that happened to do well both in its older set-up and in the newer niche. Thus according to the "palimpsest" theory some "habitus" features of older stages are always modified or lost as new habitus features come in. In the evolution of the humerus from fish to man, *anisomerism* or changing emphasis of parts has played the leading part and *polyisomerism* is seen only in the tendency to develop separate centers of ossification for the epiphysis and tuberosities.

REFERENCES TO LITERATURE

ANDREWS, CHARLES W.
1910. A descriptive catalogue of the marine reptiles of the Oxford clay. Based on the Leeds Collection in the British Museum (Natural History). London, pt. 1, xxiii + 205 pp., 94 figs., 10 pls.

ANDREWS, ROY CHAPMAN
1916. The Sei whale (Balaenoptera borealis). Mem. Amer. Mus. Nat. Hist., new ser., vol. 1, pp. 289–388, pls. 28–42.

BENSLEY, B. A.
1901. A theory of the origin and evolution of the Australian Marsupialia. Amer. Nat., vol. 25, pp. 245–269.

DE BLAINVILLE, H. M. D.
1839–1864. Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères. Paris, vols. 1–4, numerous pls. [Numerous mounted skeletons.]

BRAUS, H.
1901. Die Muskeln u. Nerven der Ceratodusflosse. Denkschr. Med. Nat. Gesellsch. Jena, vol. 4, pp. 137–300, 25 text figs., pls. 21–29.

BROILI, F.
1929. Acanthaspiden aus dem rheinischen Unterdevon. Sitz. Bayerischen Akad. Wiss., Math.-Nat. Abt., no. 2, pp. 143–163, 4 text figs., 2 pls.
1930. Neue Beobachten an *Lunaspis*. *Ibid.*, no. 1, pp. 47–51, 2 figs.
1933. Ein Macropetalichthyide aus den Hunsrückschiefern. *Ibid.*, no. 3, pp. 417–437, 7 text figs., 1 pl.

BROOM, ROBERT
1899. On the development and morphology of the marsupial shoulder-girdle. Trans. Roy. Soc. Edinburgh, vol. 38, pt. 2, pp. 749–770.
1932. The mammal-like reptiles of South Africa. London, xvi + 376 pp., figs. 1–111. [Morphology of pectoral girdle and limbs, pp. 322–330.]
1948. A contribution to our knowledge of the vertebrates of the Karroo beds of South Africa. Trans. Roy. Soc. Edinburgh, vol. 61, pt. 2, no. 21, pp. 577–629, 44 figs. [Humerus of procynodont *Leavachia*, pp. 623–626.]

BRYANT, WILLIAM L.
1919. On the structure of *Eusthenopteron*. Bull. Buffalo Soc. Nat. Sci., vol. 13, pp. 1–59, 8 figs., pls. 1–18.

COLBERT, EDWIN H.
1948. The mammal-like reptile *Lycaenops*. Bull. Amer. Mus. Nat. Hist., vol. 89, pp. 353–404, text figs. 1–24, pls. 27–34. [Pectoral girdle and fore limb, pp. 379–383; humerus in mounted skeleton, with muscle insertions, p. 399.]

CUNNINGHAM, D. J.
1903. Text-book of anatomy. New York, xxix + 1309 pp.

CUVIER, GEORGES, AND C. AND L. LAURILLARD
1849. Anatomie comparée, recueil de planches de myologie. Paris, 340 pls.

DEAN, BASHFORD
1909. Studies in fossil fishes (sharks, chimaeroids and arthrodires). Mem. Amer. Mus. Nat. Hist. vol. 9, pp. 211–287, 65 figs., pls. 26–41. [*Cladoselache* and origin of paired fins.]

DOLLO, L.
1899. Les ancêtres des marsupiaux étaient-ils arboricoles? Trav. Sta. Zool. Wimereux, vol. 7, pp. 188–203, pl. 12.
1900. Le pied du *Diprotodon* et l'origine arboricole des marsupiaux. Bull. Sci. France et Belgique, pp. 275–280.

EATON, GEORGE F.
1910. Osteology of *Pteranodon*. Mem. Connecticut Acad. Arts and Sci., vol. 2, 38 pp., 31 pls.

EHRENBERG, KURT
1938. *Austriacopithecus*, ein neuer menschenaffenartiger Primate aus den Miozän von Klein-Haderdorf bei Poysdorf in Nieder-österreich (Nieder-Donau). Sitzber. Akad. Wiss. Wien, div. 1, vol. 147, pt. 4, pp. 71–110, 9 tables. [Humerus referred by Schlosser to *Dryopithecus*.]

FRANCIS, ERIC T. B.
1934. The anatomy of the salamander. Oxford, xxi + 381 pp., 25 pls.

GILMORE, CHARLES W.
1920. Osteology of the carnivorous Dinosauria, in the U. S. National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bull. U. S. Natl. Mus., no. 110, xi + 159 pp., 79 text figs., 36 pls.

GOODRICH, E. S.
1909. *In* Lankester, Ray, A treatise on zoology. Pt. IX. Vertebrata craniata (first fascicle: cyclostomes and fishes). London, xvi + 518 pp., 515 text figs.

GREGORY, WILLIAM K.
1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. 27, pp. 1–524. [Morphology of mammalian humerus, pp. 436–437.]
1920. On the structure and relations of *Notharctus*, an American Eocene primate. Mem. Amer. Mus. Nat. Hist., new ser., vol. 3, pt. 2, pp. 51–243, pls. 23–59.
1926. The skeleton of *Moschops capensis* Broom. Bull. Amer. Mus. Nat. Hist., vol. 56, pp. 179–251, figs. 1–29, pls. 1–21. [Pectoral girdle and limb, pp. 196–211.]
1928. Were the ancestors of man primitive brachiators? Proc. Amer. Phil. Soc., vol. 67, no. 2, pp. 129–150, pls. 1–4.

1929. The muscular anatomy and the restoration of the titanotheres. *In* Osborn, Henry Fairfield, The titanotheres of ancient Wyoming, Dakota, and Nebraska. U. S. Geol. Surv. Monogr. 55, vol. 2, pp. 703–725, pls. 43, 44.

1935. Further observations on the pectoral girdle and fin of *Sauripterus taylori* Hall, a crossopterygian fish from the Upper Devonian of Pennsylvania, with special reference to the origin of the pentadactylate extremities of Tetrapoda. Proc. Amer. Phil. Soc., vol. 75, no. 7, pp. 673–690, 7 figs.

1936. Habitus factors in the skeleton of fossil and recent mammals. *Ibid.*, vol. 76, no. 4, pp. 429–444, 14 figs. [Humerus in relation to other parts, figs. 4–6, 8–12, 14.]

1946. Pareiasaurs versus placodonts as near ancestors to the turtles. Bull. Amer. Mus. Nat. Hist., vol. 86, pp. 275–326, text figs. 1–33, pls. 34, 35. [Evolution of chelonian humerus, pp. 305–307; evolution of plesiosaur humerus, p. 317.]

1947. The monotremes and the palimpsest theory. *Ibid.*, vol. 88, pp. 1–52. [Pectoral girdle and limbs, pp. 32–37, pl. 1.]

In MS. Evolution emerging: A survey of changing patterns from primeval life to man. In four parts.

GREGORY, WILLIAM K., AND CHARLES L. CAMP

1918. Studies in comparative myology and osteology. III. Bull. Amer. Mus. Nat. Hist., vol. 38, pp. 447–563, figs. 1–16, pls. 39–50. [Shoulder girdle and humerus of *Sphenodon*, *Cynognathus*, monotremes, and man, pp. 508–511, pls. 39–42.]

GREGORY, WILLIAM K., AND HENRY C. RAVEN

1941. Studies on the origin and early evolution of paired fins and limbs. Ann. New York Acad. Sci., vol. 42, pp. 273–360.

HATCHER, JOHN B., OTHNIEL C. MARSH, AND RICHARD S. LULL

1907. The Ceratopsia. U. S. Geol. Surv. Monogr. 49, xxx + 299 pp., 125 figs., 51 pls.

HEILMANN, GERHARD

1927. The origin of birds. New York, vi + 210 pp., 140 figs., 2 pls.

HEINTZ, ANATOL

1931. Untersuchungen über den bau der Arthrodira. Acta Zool., vol. 12, pp. 226–239, 2 pls.

1938. Notes on Arthrodira. Norsk Geol. Tidsskr., vol. 18, pp. 1–27, 3 pls.

1939. Cephalaspida from Downtonian of Norway. Skr. Norske Vidensk. Akad. Oslo, Mat.-Nat. Kl., vol. 1, no. 5, pp. 1–119, 35 text figs., 30 pls.

HOWELL, A. BRAZIER

1936. The musculature of antebrachium and manus in the platypus. Amer. Jour. Anat., vol. 59, no. 3, pp. 425–432, figs. 1, 2.

1937a. Morphogenesis of the shoulder architecture. Part V. Monotremata. Quart. Rev. Biol., vol. 12, no. 2, pp. 191–205, figs. 1–4.

1937b. The swimming mechanism of the platypus. Jour. Mammal., vol. 18, no. 2, pp. 217–222, figs. 1, 2.

HOWELL, A. BRAZIER, AND W. L. STRAUS, JR.

1931. The brachial flexor muscles in primates. Proc. U. S. Natl. Mus., vol. 8, pp. 1–31.

HUENE, FRIEDRICH VON
1915. On reptiles of the New Mexican Trias in the Cope collection. Bull. Amer. Mus. Nat. Hist., vol. 34, pp. 485–507, 64 figs.

HUNTINGTON, GEORGE S.
1918. Modern problems of evolution, variation and inheritance in the anatomical part of the medical curriculum. Anat. Rec., vol. 14, no. 6, pp. 359–412, 18 text figs., pls. 1–17. [Variation in the entepicondylar foramen and associated parts from *Sphenodon* to man, pp. 39–392; see fig. 15 and pls. 2–5. The median nerve and ulnar-interosseous artery pass beneath the supracondylar process or partial bridge above the former entepicondylar foramen, pl. 5.]

KELLOGG, REMINGTON
1936. A review of the Archaeoceti. Carnegie Inst. Washington Publ., no. 482, pp. i–xv, 1–366, pls. 1–37.

KIAER, JOHAN
1924. The Downtonian fauna of Norway, I. Anaspida. Skr. Norske Vidensk. Akad. Oslo, Mat.-Nat. Kl., vol. 1, no. 6, pp. 1–139, 50 text figs., 14 pls.

KLAATSCH, HERMANN
1896. Die Brustflosse der Crossopterygier. Ein Beitrag zur Anwendung der Archipterygium-Theorie auf die Gleidmassen der Landwirbelthiere. Festschrift zum 70 Geburtstage von Carl Gegenbaur, vol. 1, pp. 259–391, 42 figs., 4 pls. [*Polypterus*, musculature of pectoral limb, pls. 2, 3.]

LYON, MARCUS WARD, JR.
1913. Tree shrews: an account of the mammalian family Tupaiidae. Proc. U. S. Natl. Mus., vol. 45, pp. 1–188, pls. 1–11.

MATTHEW, WILLIAM D.
1904. The arboreal ancestry of the Mammalia. Amer. Nat., vol. 38, nos. 455–456, pp. 811–818.
1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Mem. Amer. Mus. Nat. Hist., vol. 9, pt. 6, pp. 291–565, pls. 43–52.
1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc., new ser., vol. 30, pp. i–viii, 1–510, pls. 1–65. [Primitive placental humeri, pp. 48, 117, pls. 28, 45.]

MERRIAM, JOHN C.
1908. Triassic Ichthyosauria, with special reference to the American forms. Mem. Univ. of California, vol. 1, no. 1, 196 pp., 18 pls.

MILLER, GERRIT S.
1907. The families and genera of bats. Bull. U. S. Natl. Mus., no. 57, pp. 1–282, 49 figs., pls. 1–14. [Development of trochin and trochiter on humerus, pp. 13–16.]

MINER, ROY WALDO
1925. The pectoral limb of *Eryops* and other primitive tetrapods. Bull. Amer. Mus. Nat. Hist., vol. 51, pp. 145–312, 104 text figs.

OSBORN, HENRY F.
1899. A complete mosasaur skeleton, osseous and cartilaginous. Mem. Amer. Mus. Nat. Hist., vol. 1, pt. 4, pp. 165–188, 14 figs.

OSBORN, HENRY F., AND WILLIAM K. GREGORY
1929. Mechanics of locomotion and habits of the titanotheres. *In* Osborn, Henry Fairfield, The titanotheres of ancient Wyoming, Dakota, and Nebraska. U. S. Geol. Surv. Monogr. 55, vol. 2, pp. 727–804.

OSBORN, HENRY F., AND CHARLES CRAIG MOOK
1921. *Camarasaurus, Amphicoelias,* and other sauropods of Cope. Mem. Amer. Mus. Nat. Hist., new ser., vol. 3, pt. 3, pp. 247–387, 127 figs., pls. 60–85.

PARRINGTON, F. R.
1933. On the cynodont reptile *Thrinaxodon liorhinus* Seeley. Ann. Mag. Nat. Hist., ser. 10, vol. 11, pp. 16–24, 2 figs. [Including humerus.]

ROMER, ALFRED S.
1922. The locomotor apparatus of certain primitive and mammal-like reptiles. Bull. Amer. Mus. Nat. Hist., vol. 46, pp. 517–606. [The primitive tetrahedral humerus, pp. 554–559.]
1942. Cartilage an embryonic adaptation. Amer. Nat., vol. 76, pp. 394–404.
1944. The development of tetrapod limb musculature—the shoulder region of Lacerta. Jour. Morph., vol. 74, no. 1, pp. 1–41, 18 figs.

ROMER, ALFRED S., AND L. W. PRINCE
1940. Review of the Pelycosauria. Geol. Soc. Amer., Special Papers, no. 28, 538 pp., 71 figs., pls. 1–46. [Morphology of humerus, pp. 137–144.]

SCHLAIKJER, ERICH M.
1933. Contributions to the stratigraphy and paleontology of the Goshen Hole area, Wyoming. I. A detailed study of the structure and relationships of a new zalambdodont insectivore from the Middle Oligocene. Bull. Mus. Comp. Zool. Harvard Coll., vol. 76, no. 1, pp. 1–23, 7 text figs., 1 pl. [Morphology of mole-like humeri, p. 22.]

SCHMALTZ, R.
1905, 1909. Atlas der Anatomie des Pferdes, Teil 1, Das Skelett des Rumpfes und der Gliedmassen, 1905; Teil 2, Topographische Myologie, 1909. 2. Auflage. Berlin, Schoetz.

SCHULTE, H. VON W.
1916. Anatomy of a foetus of *Balaenoptera borealis.* Mem. Amer. Mus. Nat. Hist., new ser., vol. 1, pt. 6, pp. 389–502, 10 figs., pls. 43–57.

SIMPSON, GEORGE GAYLORD
1928. A catalogue of the Mesozoic Mammalia in the geological department of the British Museum (Natural History). London, x + 215 pp., 56 figs., 12 pls. [Primitive humeri, pp. 155–160.]
1935. The Tiffany fauna, Upper Paleocene. 1. Multituberculata, Marsupalia, Insectivora and ? Chiroptera. Amer. Mus. Novitates, no. 795, 19 pp., 6 figs.
1937. The Fort Union of the Crazy Mountain field, Montana, and its mammalian faunas. Bull. U. S. Natl. Mus., no. 169, pp. i–x, 1–287, pls. 1–10. [Specialized humerus of insectivore, p. 140.]
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., vol. 85, pp. i–xvi, 1–350.
1946. Fossil penguins. *Ibid.*, vol. 87, pp. 1–100, figs. 1–33.

STENSIÖ, ERIK A:SON

1927. The Downtonian and Devonian vertebrates of Spitsbergen. Part I. Family Cephalaspidae. Skrifter om Svalbard og Nordishavet, no. 12, pt. A, text, pp. 1–391, figs. 1–103; pt. B, plates, pls. 1–112.

1931. Upper Devonian vertebrates from East Greenland. Meddel. Grønland, vol. 86, no. 1, pp. 1–212, text figs. 1–95, pls. 1–36.

1932. The cephalaspids of Great Britain. London, British Museum (Natural History), 220 pp., 70 figs., 66 pls.

STRAUS, WILLIAM L., JR.

1940. The posture of the great ape hand in locomotion and its phylogenetic implications. Amer. Jour. Phys. Anthrop., vol. 27, no. 2, pp. 199–207.

WATSON, D. M. S.

1926. The evolution and origin of the Amphibia. Croonian Lecture. Phil. Trans. Roy. Soc. London, ser. B, vol. 214, pp. 189–257, figs. 1–39.

1937. The acanthodian fishes. *Ibid.*, ser. B, vol. 228, pp. 49–146, figs. 1–25, pls. 5–14.

WHITE, ERROL I.

1946. *Jaymoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire. Geol. Mag., vol. 83, no. 2, pp. 89–97, 2 figs. [Type of new genus, family, order, Euphanerida, of ostracoderms, without armor and with well-developed fin folds.]

YOUNG, CHUNG-CHIEN

1947. Mammal-like reptiles from Lufeng, Yunnan, China. Proc. Zool. Soc. London, vol. 117, pts. 2, 3, pp. 537–597, 23 text figs., pls. 1–4. [Humeri, pp. 582–583.]